

ENVIRONMENTAL AND BIOLOGICAL CONTROLS ON THE INITIATION AND GROWTH OF A MIDDLE TRIASSIC (ANISIAN) REEF COMPLEX ON THE GREAT BANK OF GUIZHOU, GUIZHOU PROVINCE, CHINA

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ABSTRACT

The Great Bank of Guizhou (GBG) is an isolated Late Permian to Late Triassic carbonate platform in the Nanpanjiang Basin of Guizhou Province, southwest China. A faulted syncline exposes a cross section of the platform margin, including a well-preserved Anisian (earliest Middle Triassic) reef complex approximately 1 km wide and 800 meters thick. Geochronologic constraints from associated basin-margin strata indicate that reef development initiated late in the Early Triassic, making it the oldest-known platform-margin reef complex of the Mesozoic Era. The reef framework consists primarily of microspar-filled tubes ~100 μm wide and up to a few cm long that are embedded in irregular to branching, mm-scale masses of micrite, traditionally assigned to the problematic genus *Tubiphytes*. Based on preserved sporangia, the Nanpanjiang structures are interpreted as microbially induced micritic precipitates that formed in association with an otherwise uncalcified alga. A low-diversity meta-zoan and algal community also occurs within the reef complex, but these organisms did not contribute significantly to the reef framework or to the accretion of the reef complex. Rather, reef development is interpreted to have resulted largely from the stabilization of platform-margin sediments by algae and associated microbial mats. Only gradually, through the Middle and Late Triassic, did framework-building metazoans evolve to occupy and then construct reefs on the margins of carbonate platforms.

INTRODUCTION

Patterns of reef development, diversity, and ecology have been used as proxies for the health of global ecosystems through the Phanerozoic (e.g., Kiessling, 2005) and across mass-extinction events (e.g., Webb, 1998; Copper, 2001, 2002). In particular, the re-establishment of platform-margin reef complexes during the Middle Triassic, after an Early Triassic hiatus of at least 5 Ma, has been viewed as an important sign of accelerated biotic recovery from the end-Permian extinction (Flügel and Stanley, 1984; Stanley, 1988; Senowbari-Daryan et al., 1993; Flügel, 1994, 2002). In western Tethys, the oldest-known Triassic reefs are Pelsonian (Middle to Late Anisian; Flügel, 2002), formed approximately 2–3 million years after the beginning of the Middle Triassic and 7–8 Ma after the end-Permian mass extinction (based upon data from Mundil et al., 1996; Bowring et al., 1998; Mundil et al., 2004; Muttoni et al., 2004; Seeling et al., 2005). These reefs contain a moderate diversity of skeletal organisms, including scleractinian corals, calcareous sponges, mollusks, crinoids, and calcareous algae (Flügel, 2002). However, quantitative analyses of several Middle Triassic reefs and carbonate platforms indicate a limited role for macroscopic skeletal animals in constructing the reefs; despite their diversity, animals were not volumetrically significant con-

tributors of the carbonate sediment or reef framework on these platforms (e.g., Russo et al., 1997; Russo et al., 2000; Keim and Schlager, 2001). Instead, problematic framework elements, such as *Tubiphytes* and large volumes of early-marine cements, contribute most of the structure and volume to reef boundstone. Thus, although the timing of Mesozoic diversification of reef-building clades and the initiation of reef formation are similar, the degree to which the development of Middle Triassic reefs reflects the recovery of animals from the end-Permian extinction is not clear. The only Middle Triassic bioherms quantitatively dominated by skeletal invertebrates are mounds constructed by cementing bivalves of the genus *Placunopsis* from the Anisian–Ladinian Muschelkalk of eastern France and Germany (e.g., Bachmann, 1979; Hagdorn, 1982; Bachmann, 2002) and the uppermost Spathian Virgin Limestone of the western USA (S. Pruss, pers. comm., 2005) that are rarely more than a few meters in maximum dimension. These bivalve mounds aside, Anisian patch reefs exhibit higher faunal diversity and abundance than contemporaneous platform-margin reefs (Flügel, 2002). The decoupling of platform-margin reef formation from the participation of framework-building metazoans suggests the existence of important controls on Triassic platform-margin reef development beyond the evolution of animals. A satisfactory understanding of controls on the formation of Anisian platform-margin reefs cannot be obtained from the biotic record alone; information regarding environmental controls on biotic and abiotic carbonate deposition also is needed.

Only a few Anisian reefs are known in any detail, and all of these date from late in the Anisian (reviewed in Flügel, 2002). The largest of these reefs occurs in the Camorelli Limestone, a Bithynian?–Pelsonian (Middle Anisian) carbonate bank approximately 10 km across located in the southern Italian Alps. The bank was inhabited by a low-diversity biota and was rimmed, at least in part, by a *Tubiphytes*-reef margin of uncertain width (Gaetani and Gorza, 1989). Conspicuously absent from the platform are calcareous sponges and scleractinian corals (Gaetani and Gorza, 1989). Similarly, the Late Anisian–Ladinian Latemar platform in the Dolomites was rimmed by a heavily cemented, low-diversity *Tubiphytes* reef (Harris, 1993). The most abundant and diverse skeletal fauna on the Latemar occurs in slope grainstones (Harris, 1993). The Pelsonian–Illyrian (Late Anisian) Aggtelek reef, on a platform approximately 1 km across in northern Hungary, contains a greater abundance of corals, although many of these appear to have grown in relatively protected, back-reef settings (Scholz, 1972), consistent with the hypothesis that they were restricted to lower-energy environments through much of the Middle Triassic prior to acquiring algal symbionts later in the Triassic (Stanley, 1988). Like other Anisian reefs, the margin of the Aggtelek reef contains abundant marine cements, problematic organisms described by Scholz (1972) as hydrozoans, which may be *Tubiphytes*, and less-common scleractinian corals and calcareous sponges (Scholz, 1972). Late Anisian (Pelsonian–Illyrian) patch reefs containing small sponges, algae, and micro-problematica occur near Monte Verdal in the Italian Dolomites, but do

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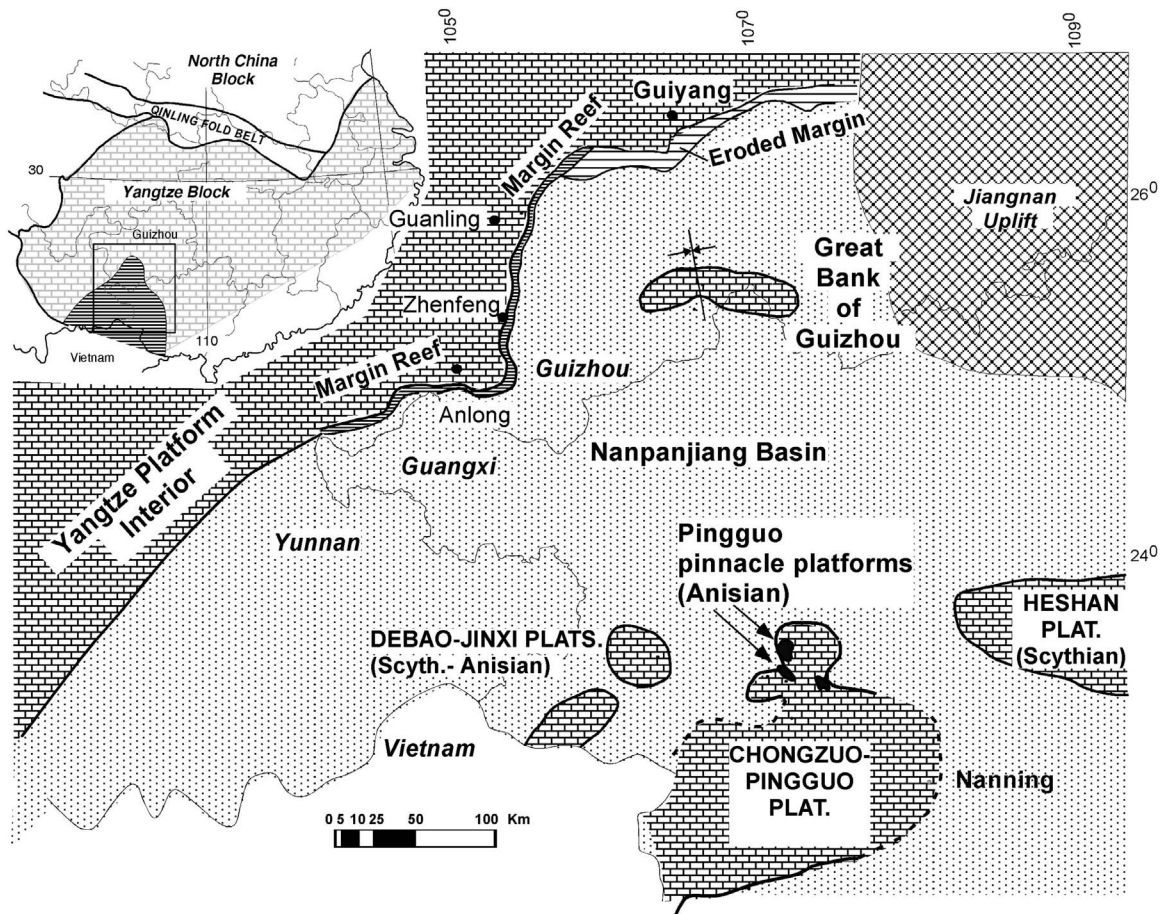


FIGURE 1—Geological map of the Nanpanjiang Basin (modified from Lehrmann et al., 2003). Inset illustrates the position of the Nanpanjiang Basin in southern China.

not exceed 10 m in diameter or 3 m in thickness (Blendinger, 1983). Similar patch reefs also are known from the Lower Muschelkalk in Poland (Szulc, 2000).

As the foregoing summary indicates, nearly all well-characterized Anisian reefs are situated in the western Tethys. Consequently, little is known about the geographic distribution of reef recovery in the Middle Triassic. Even less is known about the transition from reef-free Scythian platform margins to reef-rimmed Anisian platform margins. Lower Triassic microbial biostromes and bioherms described on the GBG (Lehrmann, 1999; Lehrmann et al., 2001; Lehrmann et al., 2003) and elsewhere (e.g., Schubert and Bottjer, 1992) have been considered reefs in some contexts (e.g., Lehrmann, 1999). However, they were generally small (less than 10–20 m thick), did not occur on the margins of carbonate platforms, and did not form environmental barriers easily discerned by differences in biofacies and lithofacies on either side. In this paper, comparisons are focused on platform-margin reefs.

Extensive Triassic reef complexes are preserved in the Nanpanjiang Basin of Guizhou, Guangxi, and Yunnan in southern China. Reefs occur on the edge of the extensive Yangtze Platform that fringed the basin and along the margins of several isolated platforms within the basin (e.g., Enos et al., 1997; Lehrmann et al., 1998; Lehrmann et al., 2003). These reef complexes add greatly to the geographic distribution of known Anisian reefs. Furthermore, they are among the oldest known Triassic reefs in the world and, unlike many of their counterparts in western Tethys, are preserved *in situ* as limestone. The Great Bank of Guizhou (GBG) contains the best-exposed reef complex among the isolated platforms because a faulted syncline exposes a two-dimensional cross-section of the platform, including Early Triassic oolite shoals and the Anisian reef margin (Lehrmann et al., 1998). Exposure of a cross-section from the plat-

form interior to the basin margin allows physical stratigraphic correlation from the massive reef complex into adjacent basin-margin clinofolds. Occurrence patterns of reef-derived grains within fossiliferous basin-margin strata provide biostratigraphic constraints on the timing of reef formation.

The purpose of this paper is to assess the stratigraphy, sedimentology, and biota of the Early and Middle Triassic platform margin of the GBG, focusing primarily on the Anisian reef complex. Reef accretion on the GBG began at or just before the Early–Middle Triassic transition. The reef contains a low diversity and low abundance of skeletal invertebrates and calcareous algae, and a high abundance of *Tubiphytes* and early-marine cements, underscoring the decoupling of reef development from metazoan evolution and participation in framework construction during the Middle Triassic. The transition from deposition of oolite shoals to a *Tubiphytes* reef near the Early–Middle Triassic boundary appears to have been controlled primarily by microbial and algal activity rather than by the advent of framework-building macroinvertebrates.

GEOLOGICAL SETTING

The Nanpanjiang Basin is a deep-marine embayment of Permian to Late Triassic age in the South China block (Fig. 1). During the Middle Triassic, the basin was located at approximately 12°N latitude and since the Triassic it has rotated approximately 90° clockwise (Enkin et al., 1992). The margin of the Nanpanjiang Basin was fringed by the Yangtze Platform, a broad carbonate platform. Late Permian transgression caused the margin of the Yangtze Platform to step back approximately 100 km (Lehrmann et al., 1998). Local areas of topographic relief along the former platform margin, in some cases fault-controlled, served as nuclei for

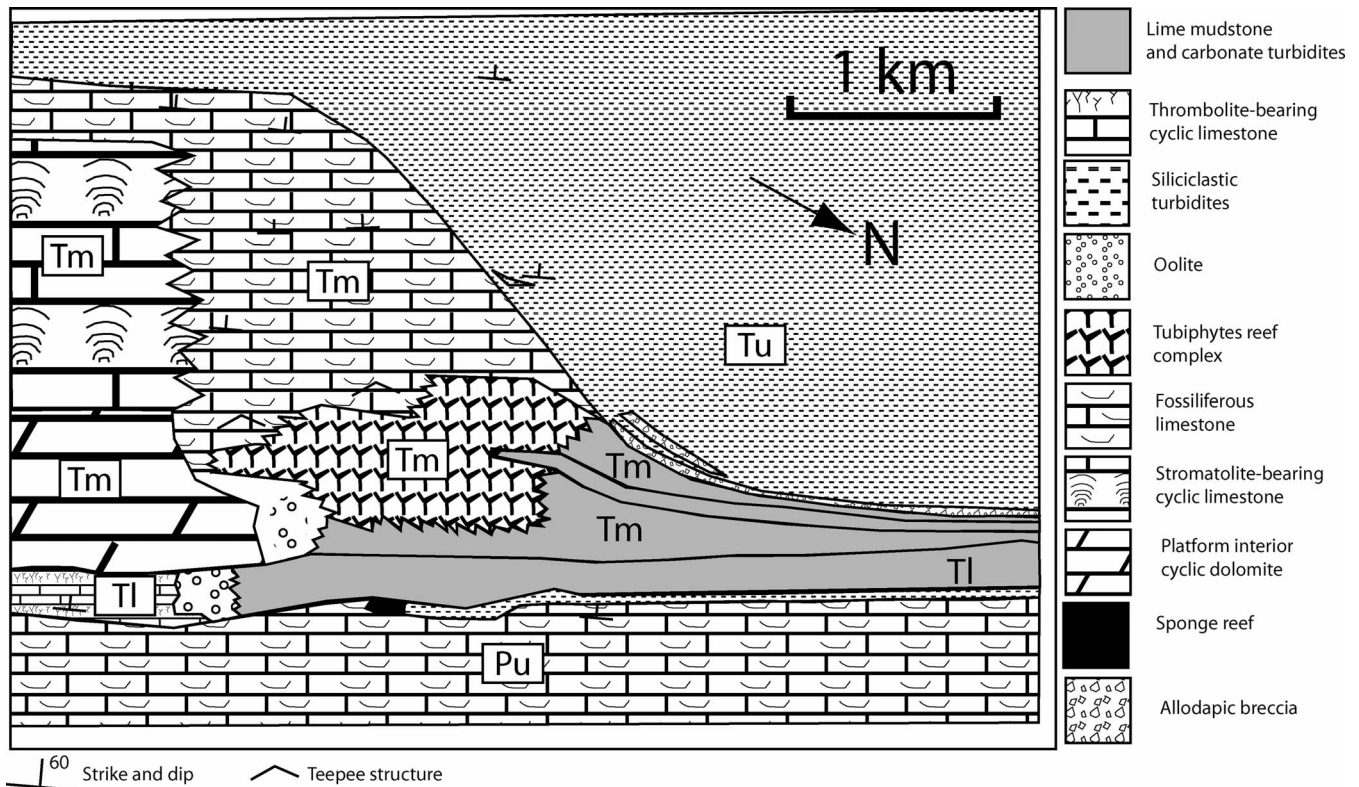


FIGURE 2—Geological map of the platform margin area of the GBG (modified from Lehrmann, 1993); Pu—Upper Permian; Tl—Lower Triassic; Tm—Middle Triassic; Tu—Upper Triassic.

several isolated carbonate build-ups, including the Debao, Chongzuo, Heshan, and Pingguo Platforms and the Great Bank of Guizhou (GBG) (Fig. 1). Middle Triassic reef complexes developed on all except the Chongzuo and Heshan platforms and, in the case of parts of the Yangtze Platform and the GBG, may have persisted into the Carnian (Late Triassic). Enos et al. (1997) discussed the stratigraphic architecture of the reef complex on the Yangtze Platform. Platform drowning on the Yangtze Platform and the isolated platforms from (modern) south to north through the Middle Triassic primarily was controlled tectonically (Enos et al., 1998; Koenig et al., 2001).

Lehrmann (1993) mapped the GBG and later published a detailed description of the platform architecture and the distribution of facies across the platform (Lehrmann et al., 1998). Subsequent work has included detailed descriptions of the Lower Triassic facies (Lehrmann, 1999; Lehrmann et al., 2001; Lehrmann et al., 2003; Yang and Lehrmann, 2003), the development of carbon isotope stratigraphy and conodont biostratigraphy for the platform (Payne et al., 2004), and quantification of the patterns of skeletal abundance through the Early-Middle Triassic recovery interval (Payne et al., 2006). Lehrmann et al. (1998) recognized a Middle Triassic platform-margin reef complex rimming the GBG exposed in cross-section on the northern margin near the town of Bianyang. South of Bianyang, the reef complex extends approximately 1 km from the platform margin toward the platform interior and is approximately 800 m thick. Because the strata dip approximately 60° to the west-southwest, a geological map of the area south of Bianyang (Fig. 2) illustrates the platform-to-basin cross section exposed regionally. Physical tracing of basin margin strata toward the platform margin indicates that the preserved reef complex is primarily Anisian (early Middle Triassic) in age (Lehrmann, 1993; Lehrmann et al., 1998).

METHODS

The large size of the Middle Triassic reef complex, its massive lithology, and its exposure in mountainous karst terrain precludes systematic

sampling along linear transects. Therefore, samples were collected where exposure permitted and where fabrics were well preserved along passable terrain in the mountains. Sample locations were recorded using a topographic map, air photos, and GPS. The distribution of samples from the reef complex is shown in Figure 3. Polished slabs and thin sections were prepared from the samples for microfacies analysis. In total, 134 polished slabs and 43 thin sections were prepared from samples collected on the GBG and 65 additional polished slabs and 38 thin sections were prepared from samples collected from Middle Triassic reefs on the Yangtze Platform near Guanling, Anlong, and Zhenfeng, as well as the pinnacle reefs on the isolated Pingguo Platform (Fig. 1). Point-counts were made on a subset of 14 samples from the GBG and visual volume estimates were made from an additional 51 samples from the GBG and other reefs.

Strata on the adjacent basin margin at the Guandao section (Fig. 2) primarily consist of carbonate turbidites containing fossil grains and clasts from the platform-margin and allodapic breccia units containing lithoclasts of platform margin and slope lithologies. Because the ages of these strata can be constrained by conodont biostratigraphy, they provide chronostratigraphic constraints on carbonate production from the reef complex.

RESULTS

Lower Triassic Platform Margin

The Lower Triassic platform margin on the GBG consists primarily of oolite shoals with subordinate molluscan shell banks. The Lower Triassic platform margin is poorly exposed in the area south of Bianyang, but platform-margin oolitic and molluscan-grainstone clasts occur in allodapic breccia deposits within Lower Triassic basin-margin strata at the Guandao section. The presence of some molluscan shell banks is indicated by rare molluscan grainstone clasts within basin-margin breccia units, one of which is more than 10 meters long and over a meter thick (Fig. 4). The occurrence of giant ooids on both the northern and southern margins of the platform indicates that oolite shoals were widespread around the

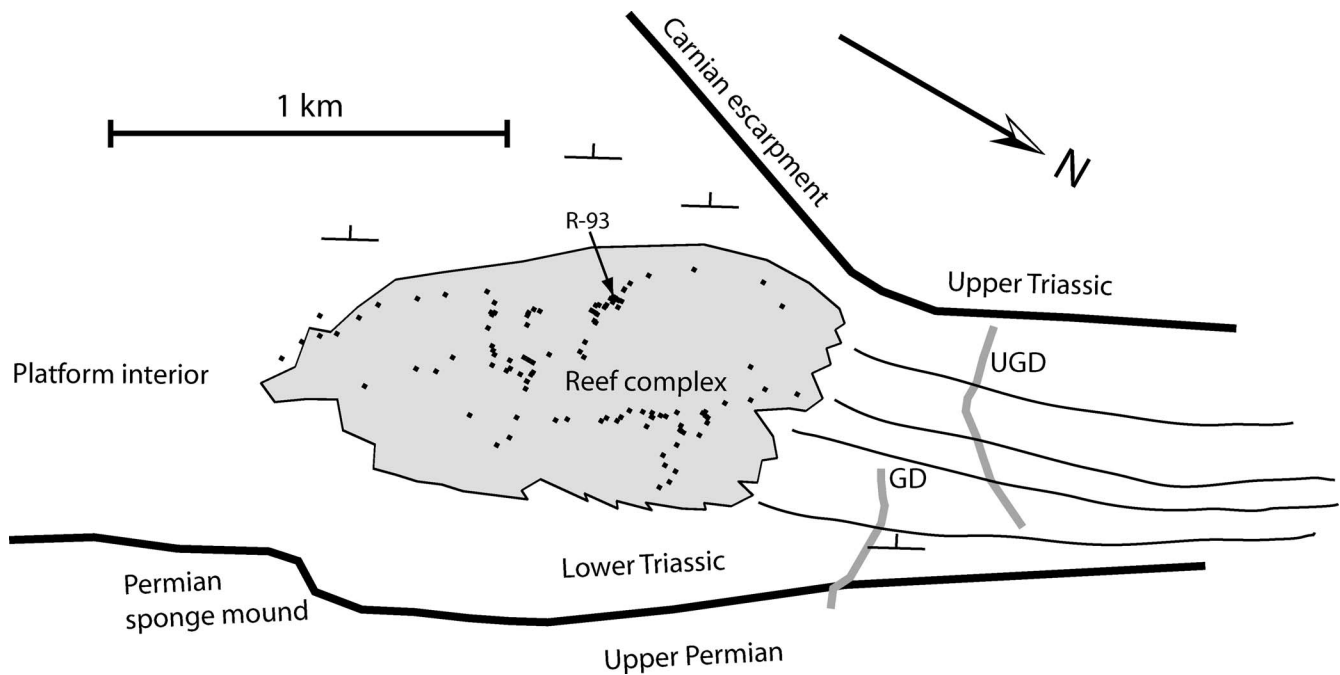


FIGURE 3—Schematic cross section of the reef complex on the GBG. Small black dots indicate the positions of samples taken from the reef complex. The position of sample R-93 discussed in the text is indicated by an arrow. Gray lines indicate the positions of stratigraphic sections on the basin margin; GD—Guandao; UGD—Upper Guandao.

platform's rim. Many of these ooids have diameters close to or exceeding 1 cm (Fig. 5A, B). By arbitrary convention, ooids are defined as <2 mm in diameter (Siewers, 2003). Similar concentrically coated grains larger than 2 mm are classified as pisoids. In the context of strata on the GBG, however, the use of the term pisoid is avoided here because of its genetic connotation with vadose pisoids; instead the coated grains >2 mm in diameter are classified as giant ooids because petrographic structures and depositional context indicate their mode of genesis was identical to that of typical ooids (see Swett and Knoll, 1989; Knoll and Swett, 1990). The occurrence of such giant ooids is notable because ooids >5 mm are extremely uncommon after the Neoproterozoic (see Flügel, 1982; Sumner and Grotzinger, 1993), although they also occur in Lower Triassic strata from the Lower Bunter of Germany (Weidlich, 2005). The giant ooids often are nucleated on the shattered cortices of other ooids (Fig. 5E), and less commonly on skeletal grains. All ooids examined from the GBG exhibit concentric laminae and tangentially oriented crystals suggestive

of an originally aragonitic mineralogy. A few also exhibit a radial fabric (Fig. 5D). The significance of the radial fabric is unclear, but may reflect originally high-Mg calcite mineralogy (Flügel, 2004). Compound ooids contain numerous smaller ooids in their cores (Fig. 5C). Consistent with field observations, point counts of breccia clasts demonstrate that ooids are much more abundant than skeletal grains within Lower Triassic platform-margin clasts in the Guandao section (Table 1). Ooids decrease gradually in proportional abundance within allodapic breccias on the basin margin at Guandao from the Griesbachian through the Smithian and are absent from younger breccia units (Table 1).

Timing of Reef Formation

Rare grains of a problematic microfossil commonly identified as *Tubiphytes obscurus* (Maslov) occur within basin-margin samples in uppermost Spathian strata, several meters below the first occurrence of the

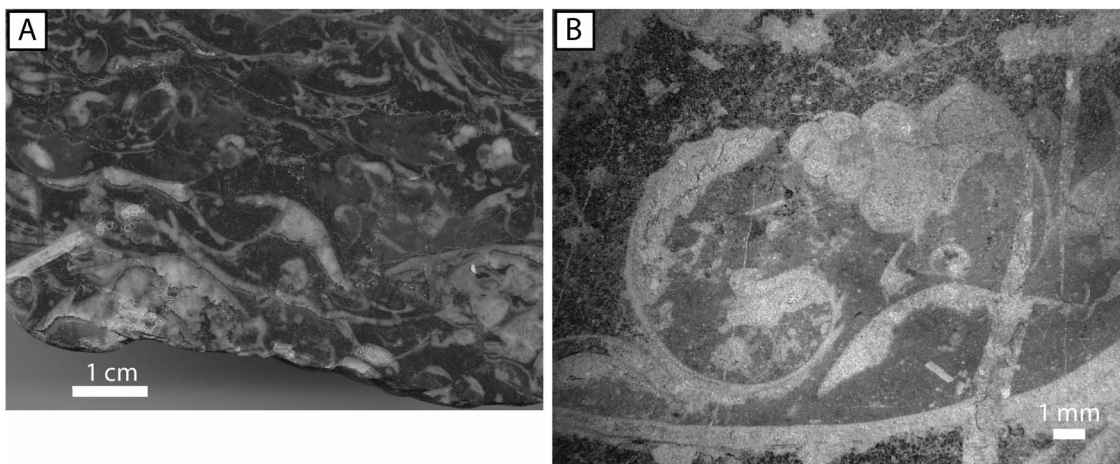


FIGURE 4—Samples of molluscan shell banks from the Early Triassic platform margin. (A) Polished slab of a breccia clast preserved within the Guandao section (PGD-79). (B) Thin section photomicrograph of the same sample.

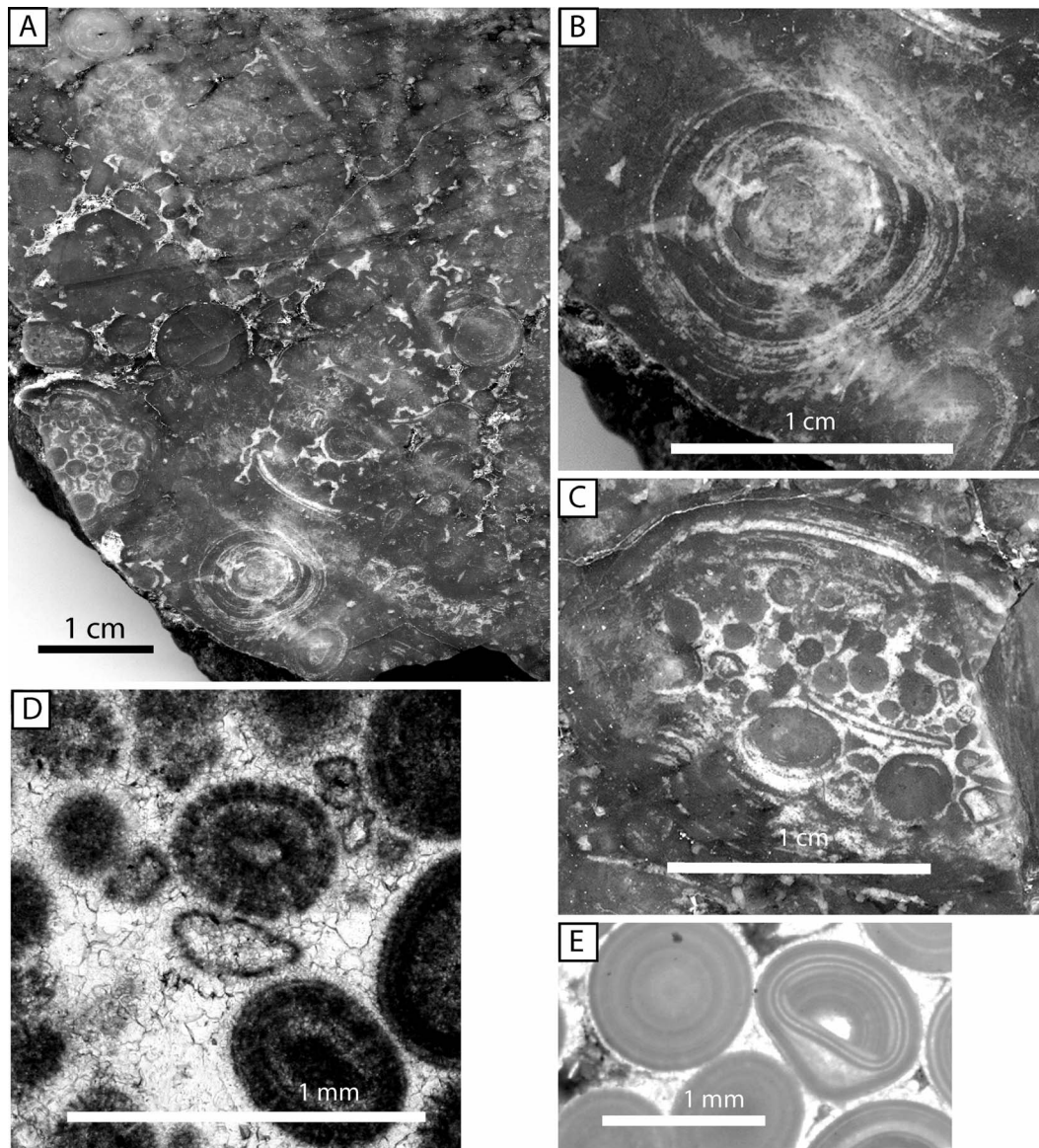


FIGURE 5—Large Early Triassic ooids from the GBG. (A) Polished slab from the southern margin of the platform. (B) Detail of giant ooid in A. (C) Detail of compound ooid in A. (D) Photomicrograph of ooids exhibiting a radial fabric (Hanlong-7). (E) Photomicrograph of an ooid nucleated on the shattered cortex of another ooid (DJ-12).

TABLE 1—Abundance of biotic and abiotic grains and cements from the Lower Triassic and Anisian platform margin. Lower Triassic data were obtained from point-counts of breccia clasts preserved on the basin margin in the Guandao section (300 points per sample, grain-solid method). Anisian data were obtained from point-counts of samples collected within the Anisian reef complex (300 points per sample, grain-solid method).

	Griesbachian N = 3	Dienerian N = 11	Smithian N = 10	Spathian N = 8	Anisian N = 14
Sparry calcite	10.7	12.1	15.4	4.2	22.4
Micrite	36	63.1	65.8	85.2	13.5
Micritic clasts	5.1	3.2	6.3	6.4	2.1
Recrystallized clasts	0	1.8	2.7	0	0
Microcrystalline cement	0	0	0	0	23.7
Fibrous cement	0	0	0	0	27.5
Ooids	42.3	16.5	9.4	0	0
Peloids	5.8	0	0	0	0
Algae	0	0	0	0	2.3
Metazoa	0	2.7	0.2	3	1.4
Foraminifera	0	0	0	0.2	0
Unidentifiable biotic	0	0.6	0.2	1	0.2
<i>Tubiphytes</i>	0	0	0	0	6.9

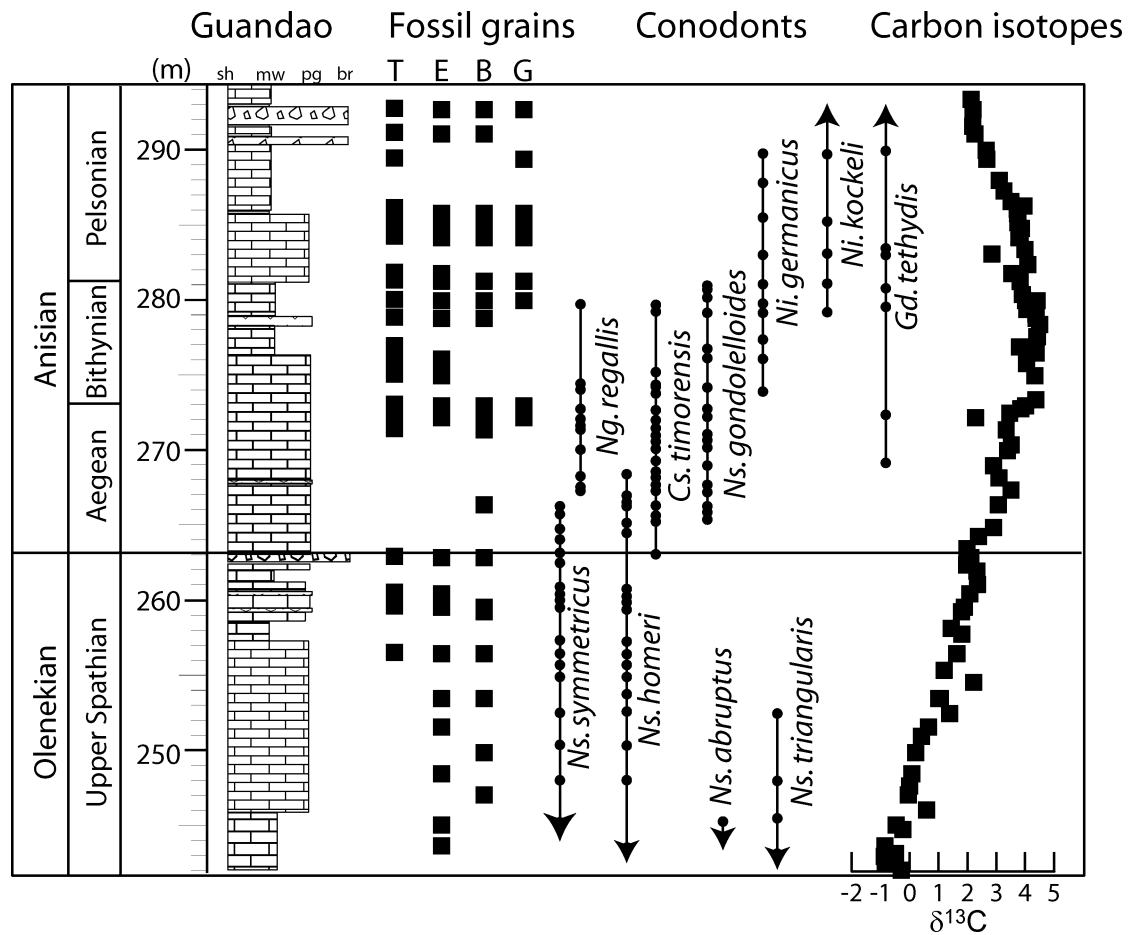


FIGURE 6—Detail of the Spathian–Anisian boundary at the Guandao section, illustrating the position of *Tubiphytes* occurrences (T) in relation to associated conodonts, other invertebrate fossil grains (E—echinoderms; B—bivalves; G—gastropods), and the carbon isotope excursion across the Spathian–Anisian boundary. Occurrence of *Tubiphytes* grains below the first occurrence of the conodont *Chiosella timorensis* indicates that reef formation began very late in the Early Triassic; carbon isotope data are from Payne et al. (2004); sh—shale; mw—mud-wackestone; pg—pack-grainstone; br—breccia.

conodont *Chiosella timorensis* (Fig. 6), the datum likely to define the Early-Middle Triassic boundary in the GSSP section (Ogg, 2004). *Tubiphytes* is characteristic of the reef-boundstone facies on the GBG and commonly is found in Middle Triassic reefs worldwide (Flügel, 2002). Figure 6 illustrates the stratigraphic position of samples containing *Tubiphytes* grains relative to both co-occurring conodonts and fossil grains, and the positive carbon-isotopic excursion across the Spathian-Anisian

boundary (see Payne et al., 2004). Examples of these oldest Triassic *Tubiphytes* grains are illustrated in Figure 7. Initial development of the reef complex near the end of the Early Triassic is consistent with the stratigraphic position of *in-situ* reef strata determined from geological mapping of the platform (Fig. 2). *Tubiphytes* grains are common in basin-margin strata from the Anisian (earliest Middle Triassic) into the Carnian (earliest Late Triassic; Fig. 8A). The abundance of *Tubiphytes* grains, determined

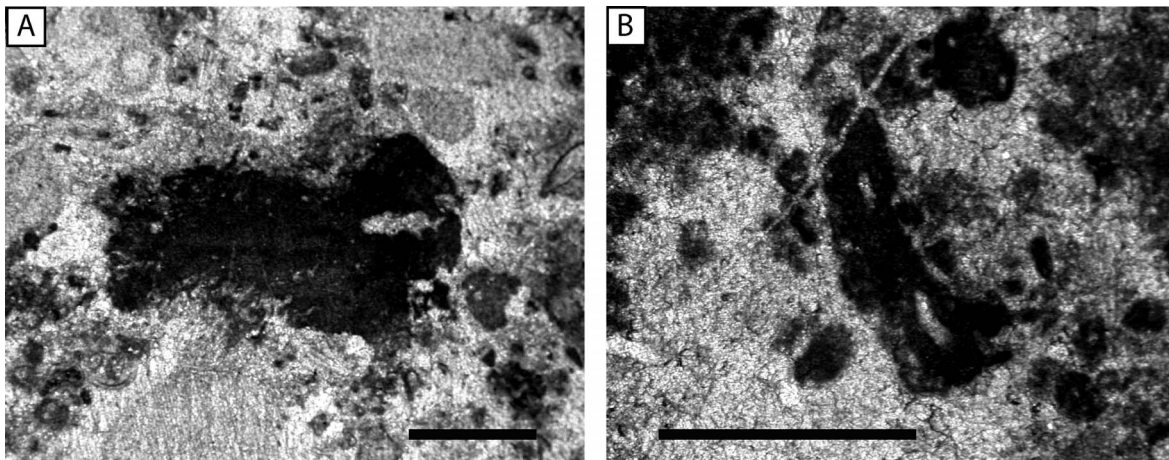


FIGURE 7—Lower Triassic specimens of *Tubiphytes* from the Guandao section; scale bars = 1 mm. (A) Sample: PGD-182. (B) Sample: PGD-186.

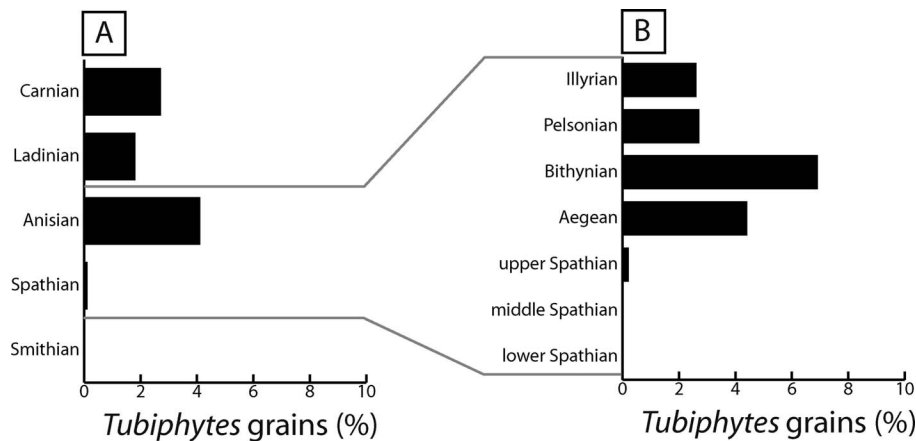


FIGURE 8—*Tubiphytes* abundance determined from point counts of 112 thin sections (73 from the Spathian–Anisian) graphed as a percent of rock volume in basin-margin strata. (A) Smithian through Carnian (300 points counted per sample; grain-solid method). (B) Detail of Spathian–Anisian interval.

from point counts, increases across the Early-Middle Triassic boundary, both within samples containing *Tubiphytes* and as a percentage of total rock volume, suggesting a rapid increase in the extent and/or rate of carbonate production on the reef complex at this time (Fig. 8B). Geological mapping indicates that the top of the preserved reef complex is late Anisian or early Ladinian in age, and that the Ladinian and Carnian platform was rimmed by a high-relief escarpment (Lehrmann et al., 1998). The presence of abundant *Tubiphytes* grains and blocks of *Tubiphytes* boundstone in Anisian through Carnian strata of the basin-margin succession indicates the persistence of a reef complex on the platform margin into the Late Triassic. Apparently, the Ladinian and Carnian reef complex was largely destroyed by erosion of fringing reefs from the Ladinian escarpment.

Lithofacies within the Reef Complex

Anisian reef facies are characterized by massive outcrop and absence of any observable bedding. Preparation of 134 polished slabs from samples collected across the reef demonstrates that the Anisian reef complex is composed of *Tubiphytes* boundstone, *Tubiphytes* grainstone, and reef-rubble breccia cemented by large volumes of isopachous marine cement. Thus, although distinct bedding planes are rare, the reef complex is interpreted to consist of lenticular zones of grainstone and reef-rubble breccia alternating with boundstone. In a few cases, clasts of reef boundstone are even incorporated into later boundstone.

Unlike the Anisian reef, blocks of reef boundstone preserved in Ladinian and Carnian allodapic breccia units in the basin-margin foreslope contain solitary and colonial scleractinian corals, sphinctozoan and inozoan sponges, and large calcareous algae (Fig. 9). The occurrence of more diverse and abundant metazoan fossils in younger reef blocks indicates that the diversity and abundance of metazoan reef dwellers and reef builders increased after the Anisian.

The Anisian reef complex contains two primary lithologies: boundstone and grainstone. The boundstone facies consists of heavily cemented *Tubiphytes* framework and contains a low abundance of skeletal grains. The grainstone contains a higher diversity and abundance of skeletal grains in addition to numerous *Tubiphytes* fragments. The biota can be separated into three guilds: framework builders, encrusters, and free-living reef dwellers (cf., Fagerstrom and Weidlich, 1999).

Framework Builders: *Tubiphytes* is the only significant element of the framework in the boundstone facies, where it contributes 5–30% of the rock volume and occurs in all samples. The occurrence of *Tubiphytes* across the reef complex indicates that it was not localized to a particular environment within the reef complex, but rather that the framework of the entire reef complex consists largely of *Tubiphytes*. *Tubiphytes* framework varies in morphology between irregularly distributed tubes (Fig.

10), clusters of smaller tubes that appear to branch into bush-like forms (Fig. 10E), and mesh-like networks of tubes (Fig. 10F). In one sample, mm-scale stromatolitic laminae overgrow sub-rounded clasts consisting of early-marine cements (Fig. 11E, F). Hemispherical fossils exhibiting a microstructure of parallel to subparallel, occasionally bifurcating tubes with tabulae are also present in a single sample (R-93) located stratigraphically high in the reef complex (Figs. 3, 11). No reproductive structures are apparent. Although the biological affinities of this fossil cannot be resolved with the material at hand, the tabulated, tubular microstructure most closely resembles chaetetids and some calcareous red algae. The trace occurrence of these fossils in the youngest part of the reef complex indicates that they did not form a vertically or laterally continuous framework and, moreover, were not involved in the initiation of reef formation or the construction of the oldest part of the reef.

Encrusters: Encrusting animals and algae are rare within the reef complex. Tubes ~200 μm in diameter similar to forms identified as *Macrotubus babai* are found in sample R-93 (Figs. 3, 12A). It is not clear whether the organisms that secreted these tubes—perhaps annelid worms—were encrusting an existing framework or creating their own vertical structure. Another problematic fossil, *Bacinella ordinata* (e.g., Mello, 1977; Pfeiffer, 1988), encrusts the *Tubiphytes* framework in the same sample (Fig. 12B–D). The continuous outer wall of the fossil, its irregular morphology, and the presence of possible chambers (e.g., Fig. 12B) suggest that it may be a sponge. It is possible that the preserved micritic structure reflects early-diagenetic precipitation of calcium carbonate around an otherwise soft-bodied organism, perhaps reflected in the discontinuous nature of the internal micritic walls. The uncertain biological affinity of this fossil and many other fossils found in the reef, however, draws attention to the absence of more familiar reef builders, such as the sphinctozoan and inozoan sponges, scleractinian corals, and calcareous red algae that are common in younger Triassic reefs. Although Latin binomials have been given to many of these fossils, the names do not always reflect a clear understanding of the organism(s) responsible. Debate over the biological affinities of *Tubiphytes* epitomizes this problem.

Reef Dwellers: A variety of fossils of free-living organisms also are found within the reef complex. The reef-dwelling fauna includes crinoids, gastropods, bivalves, ostracodes, and articulate brachiopods (Fig. 13A–D). Among the reef dwellers, crinoid grains are the most abundant, with subordinate bivalves and gastropods. Benthic foraminifera (Fig. 13E) and dasyclad algae also are present in low abundance. Fossils of free-living organisms generally occur within grainstones and are rare within *Tubiphytes* boundstone, suggesting that much of the reef-dwelling fauna lived near, but not within, the *Tubiphytes* framework.

Several generations of marine cement encrust the reef framework, often

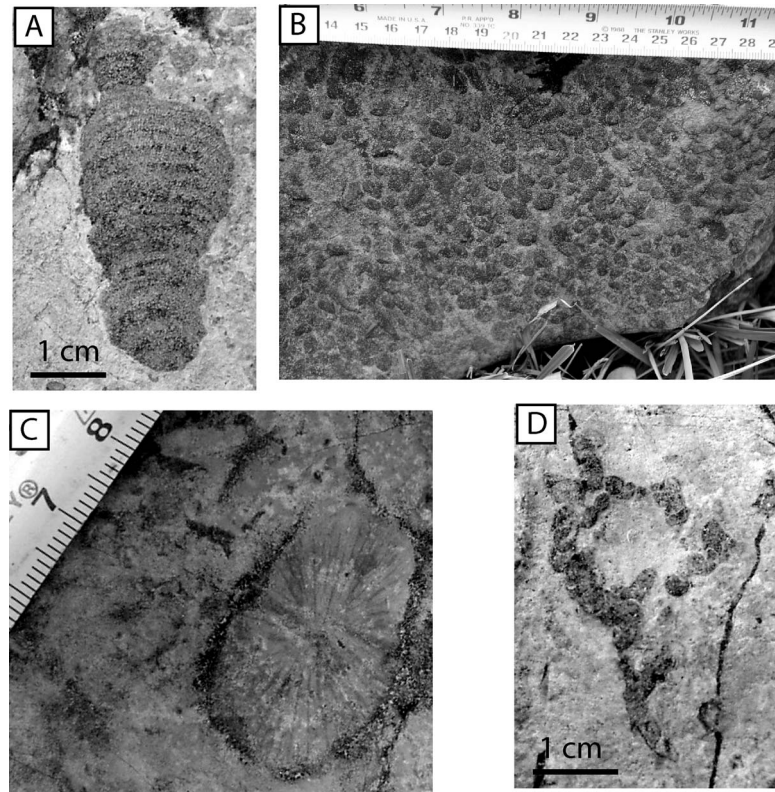


FIGURE 9—Fossils preserved in Carnian breccia clasts derived from the reef margin. (A) Calcareous red alga. (B) Colonial scleractinian coral; scale in cm. (C) Solitary scleractinian coral; scale in cm. (D) Sphinctozoan sponge.

contributing the majority of the total rock volume. In order of formation, these are: (1) peloidal-micritic cement; (2) brownish-fibrous cement; (3) isopachous-fibrous cement; and (4) botryoidal cement. What little void space remained within the reef was occluded by equant sparry calcite after burial.

Peloidal-Micritic Cement: Peloidal-micritic cement is the earliest generation of cement after the micrite that forms the tubes called *Tubiphytes*. It occurs in a large proportion of boundstone samples and consists primarily of peloidal micrite surrounding the tube-and-cement structure of *Tubiphytes* (Fig. 10). Peloidal-micritic cement appears to have played a role in the lithification of *Tubiphytes* boundstones in many cases, encrusting the tubes and bridging between tubes, adding stability to what must have been a rather fragile *Tubiphytes* framework. The fragility of *Tubiphytes* as a framework-builder is also suggested by the large proportion of *Tubiphytes* grains in grainstone samples that are not encrusted with cements (Fig. 14). *Tubiphytes* grains encrusted only by peloidal-micritic cement are found in basin-margin turbidite deposits (Fig. 10B), providing further indication that cementation occurred prior to any significant burial.

Brown-Fibrous Cement: Brownish-fibrous cements occur within the boundstone facies as well. These cements always post-date the peloidal-micritic cements, and there is no evidence for dissolution between the deposition of micritic cement and fibrous cement (Fig. 10A, B). Brownish-fibrous cement is volumetrically significant within the boundstone facies and often occludes much of the remaining volume after the *Tubiphytes* framework and peloidal micritic cement. Because there is no evidence of dissolution prior to their deposition, brown-fibrous cement is interpreted as penecontemporaneous cement deposited when the reef was still in active contact with seawater. Consistent with this interpretation, brownish-fibrous cement encompasses *Tubiphytes* in some grains preserved within basin-margin turbidites (Fig. 10).

Isopachous-Fibrous Cement: Isopachous-fibrous cement fills cavities within the reef boundstone as well as the voids between clasts in reef-

rubble breccias (Fig. 15). Within the reef-rubble breccia, isopachous cement may contribute more than 50% of the rock by volume (Fig. 15C, D, E). In some cases, dissolution clearly preceded precipitation of the cement as demonstrated by the truncation of fossil grains and sedimentary fabric in the surrounding boundstone (Fig. 15). In other samples, there is no clear evidence for dissolution before precipitation of isopachous cement. Isopachous cement commonly contains dark- and light-colored bands indicating several episodes of cement precipitation. In a few cases, micritic sediment accumulated within voids between episodes of cementation (Fig. 15B). The deposition of micritic sediment between generations of fibrous cement indicates cementation occurred while the voids were still open to shallow-marine waters. Because the isopachous cements post-date peloidal-micritic and brownish-fibrous cement (and possibly botryoidal cements), all of these generations of cement are likely to have precipitated in shallow-marine settings prior to significant burial. However, the absence of clasts containing isopachous cements within basin-margin turbidites suggests that these cements did not form on the sea floor, but rather within the lithified reef complex or as shallow-burial marine cements.

Botryoidal Cement: Botryoidal cements are common within the boundstone facies. They range in size from less than 1 cm up to approximately 5 cm, appear dark on polished slabs (Fig. 16), and radiate from a single point of nucleation on the substrate. These originally aragonitic cements always post-date micritic cements when a temporal relationship can be established and post-date fibrous cements in some instances. The botryoids are most likely marine-phreatic cements deposited within the lithified reef or during early burial.

Equant-Sparry Calcite: Sparry calcite is a minor component of the reef complex found primarily within framework voids that were not completely filled by isopachous-fibrous cement (Fig. 15A, B). Sparry calcite is typically interpreted as a diagenetic phase precipitated during burial (Flügel, 2004). There is no evidence to contradict this interpretation in the case of the Anisian reef on the GBG. The low abundance of sparry

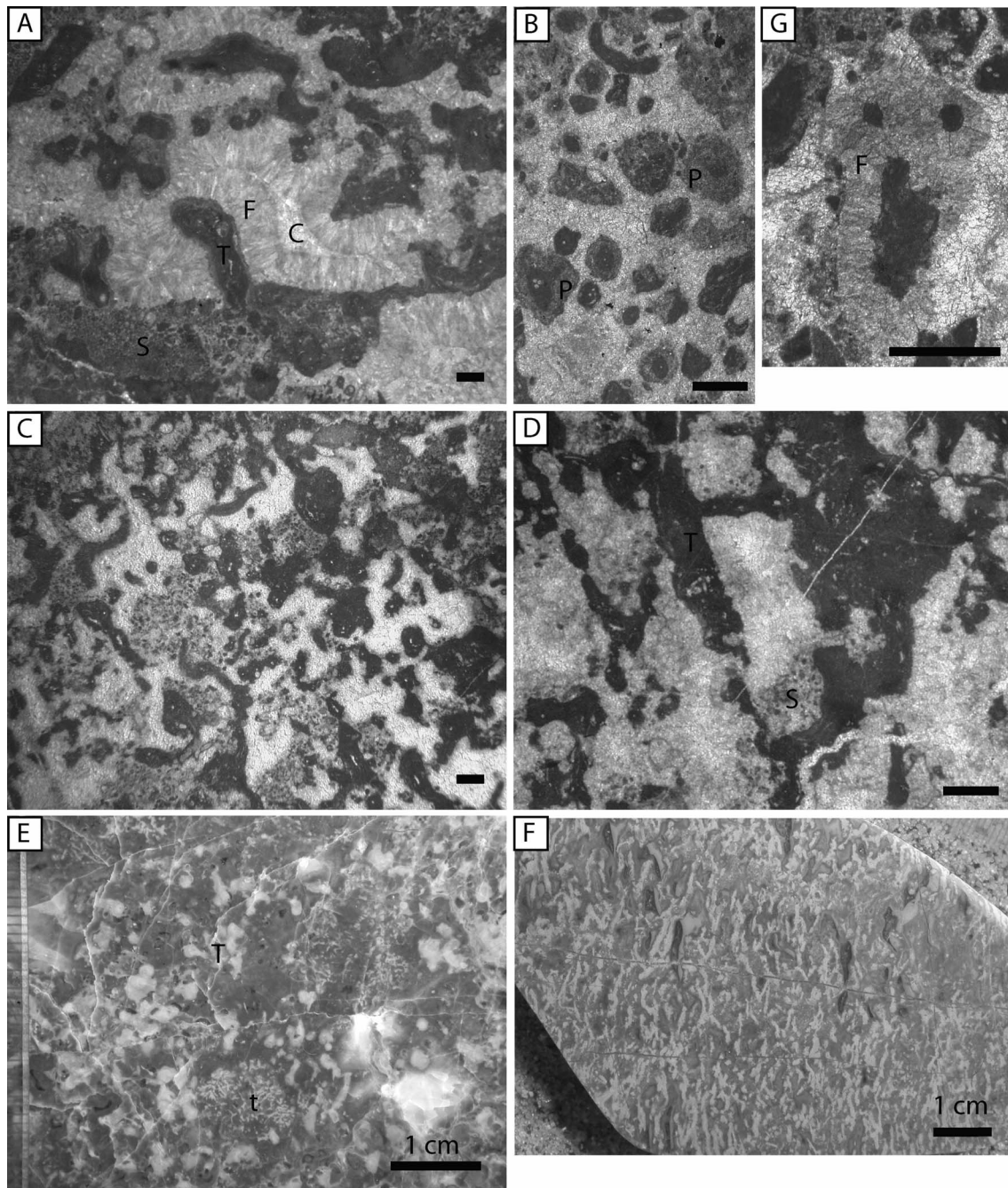


FIGURE 10—Photomicrographs illustrating *Tubiphytes* framework in the boundstone facies. S—internal sediment; T—*Tubiphytes*; F—fibrous calcite cement; C—sparry calcite; P—peloidal micritic cement; t—smaller *Tubiphytes*; scale bars=1 mm. (A) Framework encrusted by micritic cement and brownish-fibrous cement, with a small void filled by diagenetic equant-sparry calcite (Reef 6–14). (B) Basin margin grainstone containing *Tubiphytes* fragments encrusted by peloidal-micritic cement (PGD-227). (C) Irregular *Tubiphytes* framework with peloidal-micritic internal sediment (R-74). (D) Interconnected *Tubiphytes* framework illustrating the irregular shape of the micritic tubes and presence of larger micritic masses without an obvious central tube (R-93). (E) Polished slab illustrating two sizes of micritic tubes. The cluster of smaller tubes in the lower center of the picture exhibits a bush-like branching form (HY-5). (F) Polished slab of *Tubiphytes* framework from the Pingguo Platform (ALT-5–66). (G) Basin margin grainstone sample containing a clast of *Tubiphytes* encrusted by brownish fibrous cement (PUG-15).

cement indicates that most of the reef framework was occluded prior to burial by the several generations of early-marine cements.

In summary, the history of cementation of the *Tubiphytes*-reef complex is interpreted as follows (see Table 2). The earliest generation of carbonate precipitation is the micritic envelope of *Tubiphytes*. This envelope is interpreted to reflect microbially mediated carbonate precipitation around a soft-bodied alga to form the framework (see discussion of *Tubiphytes* below). Precipitation of the micritic envelope of *Tubiphytes* must have occurred during or at the conclusion of the life of the alga. The second

generation of cement consisted of peloidal micrite surrounding the *Tubiphytes* framework. Peloidal-micritic cement formed *in situ*, often surrounding the *Tubiphytes* framework. Precipitation of peloidal-micritic cement may have been biologically mediated, although traces of microbial filaments are not preserved within it. The subsequent generation of brownish-fibrous marine cement shows no evidence for dissolution prior to precipitation and is found surrounding *Tubiphytes* in grains transported to the basin margin in turbidity currents. These two pieces of evidence indicate that even the brownish-fibrous cement was precipitated

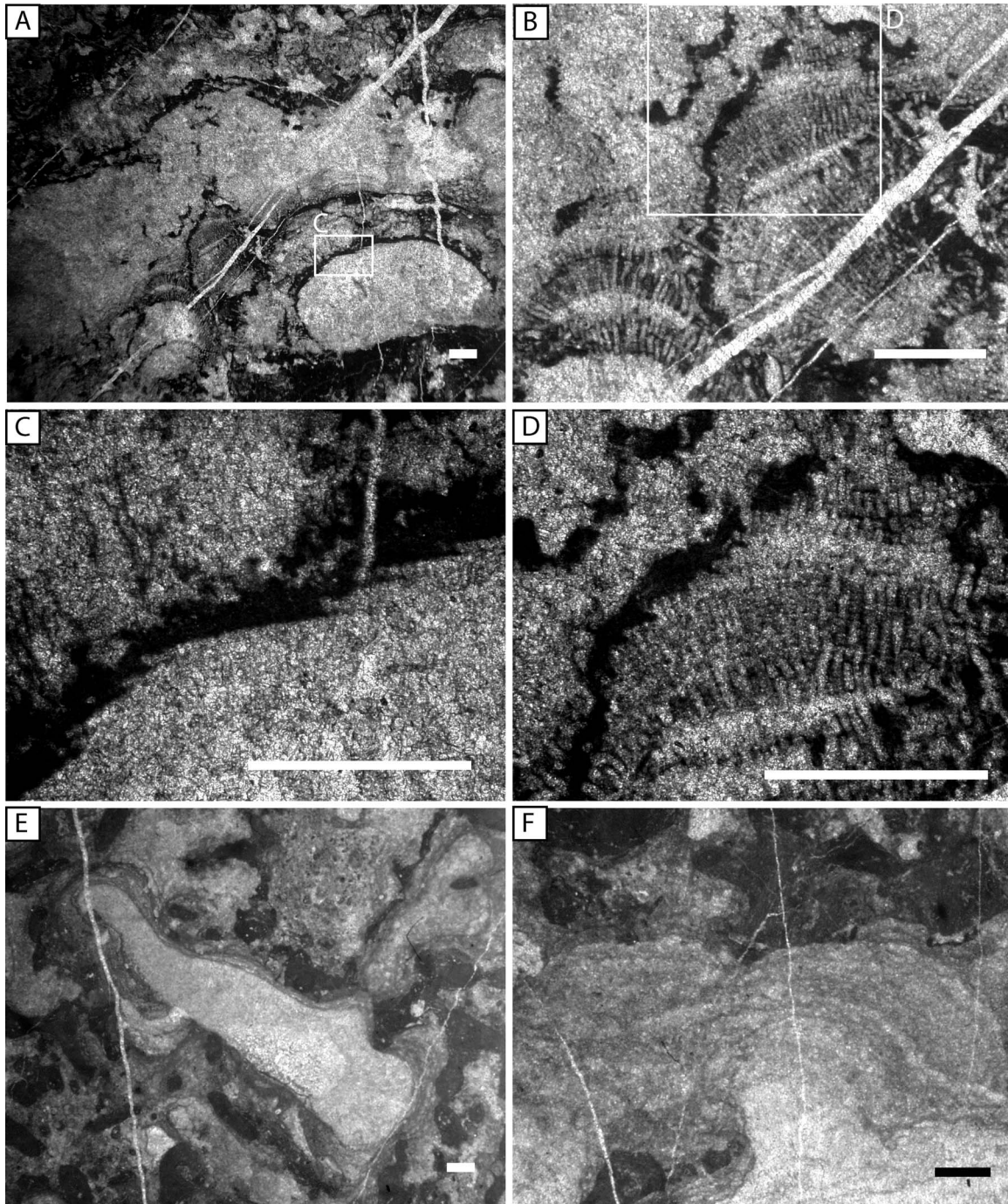


FIGURE 11—Other framework builders in the reef; scale bars=1 mm. (A) Problematic, recrystallized, framework-building fossil (R-93). (B) Another specimen of the problematic fossil from the same sample (R-93) illustrating the internal tubular structure. (C) Detail of A, illustrating the layered morphology. (D) Detail of B, illustrating the tubular microstructure at higher magnification. (E) Stromatolitic laminae and *Tubiphytes* encrusting a clast composed of brown-fibrous cement (Reef 3–6). (F) Detail of stromatolitic laminae in the same sample.

penecontemporaneously, probably as aragonite, in open contact with seawater prior to any significant burial. Given the generally high depositional rates of approximately 200 m/Ma in the reef complex, open contact with seawater is likely to have lasted on the order of 10^3 – 10^4 years. Evidence for dissolution before the precipitation of isopachous-fibrous cements suggests possible exposure or burial of the reef boundstone prior to this episode of cementation. On the other hand, if the micrite deposited between layers of isopachous cement in some cavities is derived directly from sediment on the seafloor, then, at least in some cases, the isopachous cement also may have been precipitated in contact with shallow marine

water. Botryoidal-aragonite cement post-dates isopachous cement in several samples and likely reflects continuing carbonate precipitation during early burial. Finally, the remaining voids were occluded completely by sparry calcite after burial.

Geological mapping demonstrates ~400 meters of relief between the reef complex and the adjacent basin-margin toe-of-slope. The restricted lagoonal facies within the Middle Triassic platform interior (Lehrmann et al., 1998) further demonstrate that the reef complex was of sufficient extent to restrict water flow through the platform interior. However, there is little direct evidence observable in the field that the *Tubiphytes*

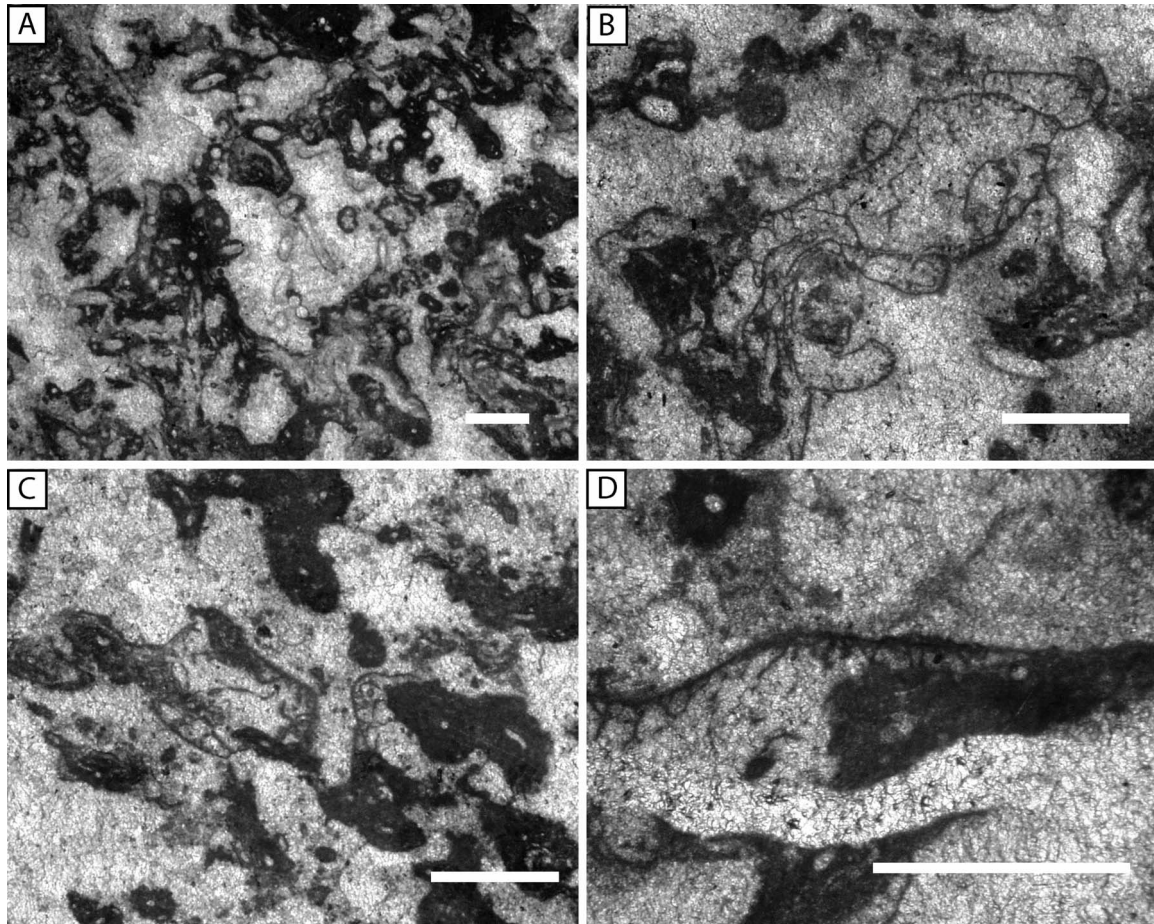


FIGURE 12—Problematic forms found within the boundstones, sample R-93; scale bars = 1 mm. (A) Encrusting or framework-building tubes, similar to *Macrotubus*. (B) Problematic encrusting organism, possibly *Bacinella*. This organism may be a sponge, given its continuous outer surface. (C) Problematic encrusting organism, possibly *Bacinella*, likely the same as in B. (D) Problematic organism, likely the same as in B and C, encrusting *Tubiphytes*.

framework obtained any significant relief within the reef complex itself. Local relief of less than one meter does occur in the form of hemispherical *Tubiphytes* bioherms in contact with grainstones (Fig. 17). Unfortunately, karst weathering and locally thick vegetation preclude determination of detailed stratigraphic relationships within the reef complex over distances greater than a few tens of meters.

Morphological Evidence for the Formation of *Tubiphytes*

Tubiphytes, a problematic microfossil, is by far the most-important framework builder and sediment contributor (other than cements) within the reef complex. Lehrmann (1993; see also Lehrmann et al., 1998; Fig. 8D) first identified and figured spherical bodies $\sim 500 \mu\text{m}$ in diameter in a specimen of *Tubiphytes* from a reef-boundstone sample taken on the GBG. Several smaller spherical bodies, $\sim 50 \mu\text{m}$ in diameter, are attached to the inner wall of the larger sphere. These spherical structures most commonly occur at the branch junctions of *Tubiphytes* tubes. During this study, more extensive investigation of reef samples, as well as *Tubiphytes* fragments transported to the basin margin on the GBG, has yielded numerous similar specimens, several of which are illustrated in Figure 18. The micrite envelope of *Tubiphytes* has an irregular outer surface and commonly contains $\sim 10\text{-}\mu\text{m}$ filaments within the micrite envelope (Fig. 19A, B).

Spherical structures containing multiple internal spheres also occur in Middle Triassic limestone from the Dolomites, but not associated with *Tubiphytes*; instead, they occur only as isolated bodies. The specimens from the Dolomites have been interpreted as reproductive bodies produced by dasyclad algae because they bear close resemblance to the spo-

rangia of extant dasyclads, such as *Acicularia* (Pugliese, 1997), and because dasyclad algae are found in the same samples, though never physically connected to the spherical structures.

The biological affinities of fossils identified as *Tubiphytes* in the Paleozoic and Mesozoic have been controversial (see, e.g., Riding and Guo, 1992; Senowbari-Daryan and Flügel, 1993; Wang et al., 1994; Vachard et al., 2001), as have the parts of the structure to which the name *Tubiphytes* applies. The original definition of *Tubiphytes* proposed by Maslov (as translated in Senowbari-Daryan and Flügel, 1993) applied only to the outer micritic crust (Senowbari-Daryan and Flügel, 1993); the central tube was considered to represent space occupied by a soft-bodied organism that was encrusted by a microbe or microbial community. Subsequent attribution of these fossils to hydrozoans and sponges (see summary in Senowbari-Daryan and Flügel, 1993) implied that the central tube instead represented a canal system within an organism rather than space occupied by a separate entity. In a review of Paleozoic specimens of *Tubiphytes*, Senowbari-Daryan and Flügel (1993) concluded that Paleozoic specimens consist of microbially mediated micrite precipitated around an unpreserved, soft-bodied organism. No consensus on the higher-level taxonomic assignment of Paleozoic *Tubiphytes* exists, however, because several other workers (e.g., Riding and Guo, 1992; Wang et al., 1994) favor poriferan affinities for *Tubiphytes*. Given the uncertain biological affinities of these fossils, it also is not clear (and is perhaps unlikely) that all of the species of fossils assigned to the genus *Tubiphytes* are the remains of the same or closely related organisms.

In the case of the Middle Triassic reef-framework structures, however, it may be possible to narrow their origin further. There are four possible

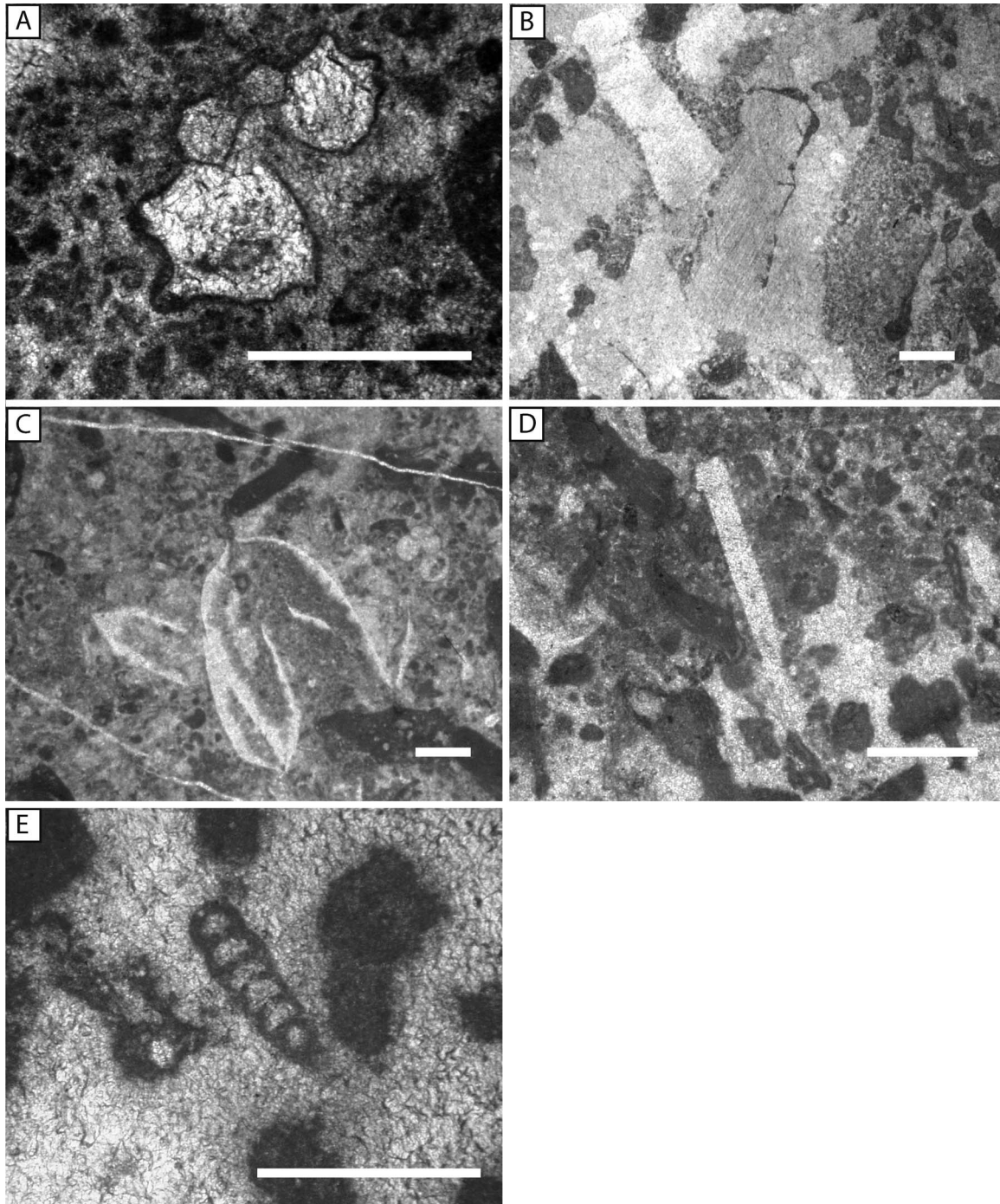


FIGURE 13—Reef-dwelling organisms; scale bars = 1 mm. (A) Small, ornamented gastropod (R-74). (B) Partially disarticulated crinoid columnals (R-85). (C) Small, thin-shelled bivalves (Reef 1–1). (D) Echinoid spine in a *Tubiphytes* grainstone (Reef 2–3). (E) Uniserial foraminiferan in a *Tubiphytes* grainstone (R-74).

alternatives for the formation of *Tubiphytes*, and the same explanation need not apply to all localities or time intervals. *Tubiphytes* may be an animal with a skeleton, an animal covered by diagenetic carbonate, a skeletal alga, or an alga covered with diagenetic carbonate. The irregular filaments preserved within the micrite envelope indicate the presence of microbes and, therefore, eliminate the skeletal options. The 0.5-mm spherical structures containing multiple smaller spheres attached to their inner walls bear striking similarities to algal sporangia, suggesting an algal origin. Moreover, the authors are unaware of any comparable structures produced by animals. Consequently, the *Tubiphytes* structures in these samples are interpreted to reflect diagenetic precipitation of micritic

cement, likely microbially induced, around an otherwise soft-bodied filamentous alga. Localization of microbial mats around soft-bodied algae can be explained by the availability of excreted algal metabolites (e.g., Stabenau and Winkler, 2005), another feature that cannot be accounted for easily if *Tubiphytes* is of animal origin. The algal/microbial interpretation is supported further by the occurrence of irregular bodies of micrite that are otherwise indistinguishable from the micritic envelope of *Tubiphytes*. Some of these bodies contain stromatolitic laminae (Fig. 19C, D) that are not associated with any obvious tubes or cylindrical morphology and are too large to represent tangential sections of *Tubiphytes* tubes.

The interpretation presented above is similar to the interpretation

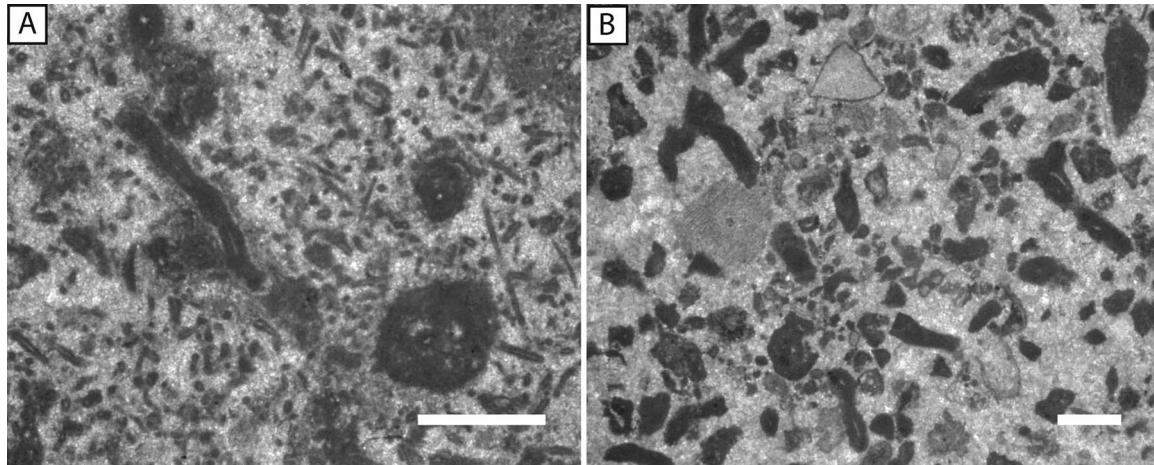


FIGURE 14—*Tubiphytes* and fossiliferous grainstones; scale bars=1 mm. (A) *Tubiphytes* grainstone containing micritic tubes of three distinct diameters (Reef 6–14). (B) *Tubiphytes* grainstone containing a crinoid columnar and other echinoderm debris (Reef 8–18).

favored by Senowbari-Daryan and Flügel (1993) for many Paleozoic fossils identified as *Tubiphytes*. However, spherical structures containing internal spheres have not been reported in Paleozoic specimens of *Tubiphytes*, the micritic envelope tends to have a more uniform fabric in older samples, and the outer edge of the micritic envelope in Paleozoic specimens tends to be smoother and more clearly defined than in Middle Triassic specimens. More detailed analysis is needed to establish the generality of the algal/microbial interpretation for Middle Triassic fossils identified as *Tubiphytes* and to determine potential biological affinities (or lack thereof) between Paleozoic and Mesozoic *Tubiphytes*, both in terms of the mode of formation and specific taxonomic relationships of the organisms responsible.

Observations from Other Platforms in the Nanpanjiang Basin

Platform-margin reefs around the Nanpanjiang Basin, including reefs on the Pingguo Platform and several localities on the margin of the Yangtze Platform (Fig. 1), contain lithologies and biotic assemblages similar to those found on the GBG. In particular, the primary framework element of every reef is *Tubiphytes*. Preliminary observations indicate that the diversity of framework elements within the Yangtze Platform reefs is greater than on the GBG, whereas the pinnacle reefs on the Pingguo Platform contain a more-similar, low-diversity, heavily cemented reef facies (Christensen and Lehrmann, 2004). Christensen and Lehrmann (2004) determined via visual estimates of thin sections that marine cements contributed ~50% of the reef volume on the isolated platforms (the GBG and Pingguo Platform), but only 20–30% of the reef volume at four localities on the Yangtze Platform. The higher proportion of cement on the isolated platforms is coupled with a lower abundance of framework elements (10–15%) than on the Yangtze Platform (18–35%). Furthermore, *Tubiphytes* was the only significant framework element on the isolated platforms, in contrast to additional contributions from scleractinian corals, calcareous sponges, and solenoporacean algae on the Yangtze Platform. Factors responsible for differences in diversity and abundance likely include differences in the ages of the reefs (e.g., some of the more diverse reefs on the Yangtze Platform may be primarily Ladinian in age, whereas the Pingguo reef is Anisian), and their positions on the platforms.

DISCUSSION

The Anisian reef on the GBG bears strong qualitative and quantitative resemblance to other Middle Triassic reefs throughout Tethys. Shared features include the *Tubiphytes* framework, large volumes of early-marine cements, and the gradual integration of large skeletal metazoans into the

reef framework through the Middle and Late Triassic (e.g., Flügel and Stanley, 1984; Stanley, 1988; Flügel, 2002). Parallels between the reef on the GBG and those from western Tethys are reflected in quantitative studies of reef and platform composition. *Tubiphytes* is the dominant component of the reef framework; animals constitute only a few percent of the rock volume. For example, Keim and Schlager (2001) found that platform-margin reef facies on the Sella Massif contained more than 40% marine cement. On the Marmolada Platform, Blendinger (1994) determined that the reef and slope facies consisted of nearly 40% early-marine cements and another 17% consisted of crusts, which also may be interpreted as early-micritic cements. Harris (1993) estimated that 20–40% of the boundstone facies on the Latemar consisted of early-marine cements. All of these values are consistent with values of 20–50% early-marine cement in the reefs of the Nanpanjiang Basin. Furthermore, less than 10% of the reef volume in all of these localities consists of metazoan skeletal framework. For example, only 5–6% of the rock volume consists of skeletal grains in boundstone samples from Middle Triassic reefs and reef blocks from the Sasso Lungo (Russo et al., 1997) and Marmolada (Russo et al., 2000) platforms.

The qualitative and quantitative resemblance of the Anisian reef on the GBG to Middle Triassic reefs in the western Tethys suggests that patterns and processes of reef formation on the GBG are representative of controls on the re-development of reefs throughout Tethys, if not globally. Therefore, the search for controls underlying the patterns observed on the GBG should include processes acting on the regional to global scale. Both oceanographic and biological factors may have promoted the intense cementation observed on Middle Triassic carbonate platforms. The insignificance of pelagic organisms as sinks for calcium carbonate before the evolution of coccolithophorids relegated nearly all carbonate precipitation to shallow-shelf environments, primarily in the tropics. The lack of significant continental flooding at this time further reduced the surface area upon which calcium carbonate could be precipitated from seawater. Because carbonate deposition must balance the delivery flux of carbonate alkalinity over geological timescales, the rate of carbonate precipitation per unit area on the shallow tropical shelf must have been high to balance the delivery of carbonate alkalinity from weathering (Ridgwell, 2005). All else being equal, these factors should have increased the average carbonate saturation state of the tropical surface ocean—a condition further enhanced by the minor input of enzymatically controlled skeletal carbonates to the carbonate factory. Many of the same factors may account for the large volumes of cement in Permian reefs (e.g., Grotzinger and Knoll, 1995). Volumetrically significant cementation of reefs from other intervals with different boundary conditions of sea level and biological carbonate production, such as Devonian reefs in South China (e.g.,

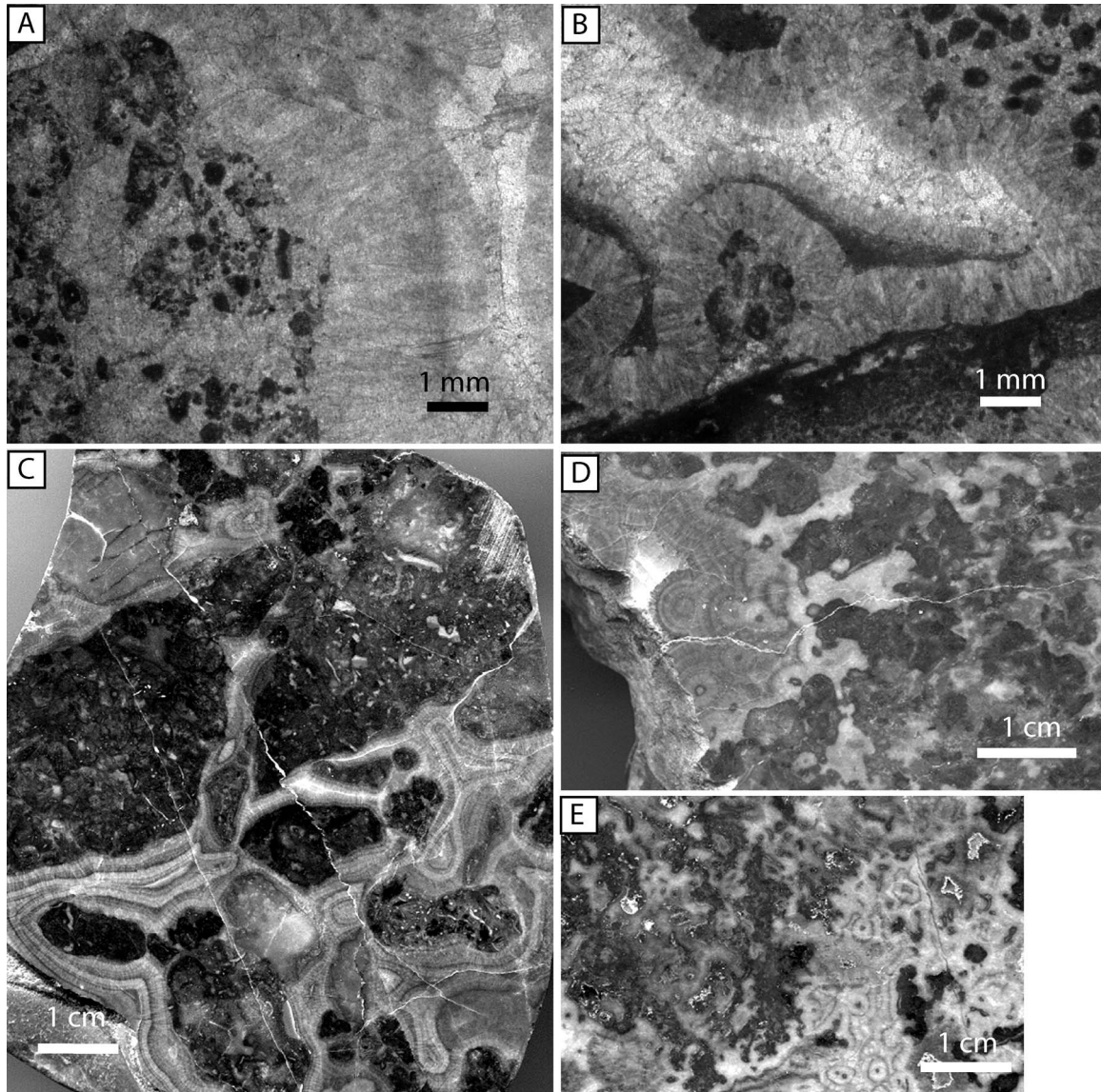


FIGURE 15—Isopachous-fibrous cements. (A) Sample illustrating dissolution prior to deposition of fibrous cement; note truncated grainstone fabric on the left side of the sample (R-82). (B) Sample illustrating multiple episodes of cement deposition, with the deposition of micritic sediment on the floor of the cavity between episodes of cement precipitation (Reef 5–15). (C) Slab photo of reef-rubble breccia cemented by isopachous-marine cement (Reef 12–01). (D) Slab photo of *Tubiphytes* boundstone cemented by dark-colored peloidal-micritic cement and later isopachous marine cement (R-7). (E) Slab photo of *Tubiphytes* boundstone cemented by dark-colored peloidal-micritic cement and light-colored isopachous-marine cement (R-9).

Shen and Webb, 2004) and Australia (Wood, 1998), indicate that other factors, including the rate of framework production, rate of creation of accommodation space, margin geometry, and water circulation, exert important controls on cementation (Seeling et al., 2005).

The factors promoting early cementation on the platform margin, however, cannot explain the global absence of similar reefs during the Early Triassic. The same conditions that account for intense cementation in Permian and Middle Triassic reefs—limited epicontinental seas and the absence of pelagic carbonate producers—also characterized Early Triassic oceans. Moreover, the abundance of skeletal grains was unusually low in Early Triassic shelves and platforms (Payne et al., 2006). Lower Triassic carbonate precipitates do occur both in the form of seafloor aragonite fans and oolite beds just above the end-Permian extinction horizon (Kershaw et al., 2002; Ezaki et al., 2003; Heydari et al., 2003; Lehrmann et al., 2003; Groves and Calner, 2004), and as locally abundant seafloor precipitates (Woods et al., 1999), precipitated microbialites (Schubert and Bottjer, 1992; Baud et al., 1997; Sano and Nakashima, 1997; Lehrmann, 1999; Lehrmann et al., 2001; Pruss and Bottjer, 2004), and oolites (Brog-

lio Loriga et al., 1982; Lehrmann et al., 2001) throughout the Lower Triassic. On the GBG and Pingguo platforms in the Nanpanjiang Basin, for example, Early Triassic platform margins consisted primarily of oolite shoals, particularly from the Griesbachian through the Smithian. The transition from an Early Triassic platform margin dominated by oolites to a Middle Triassic margin consisting of a heavily cemented reef complex, however, requires explanation.

The most important factor facilitating the establishment of the Anisian reef on the GBG appears to be the presence of *Tubiphytes*. The absence of *Tubiphytes* framework on the GBG and elsewhere during the Early Triassic, and the presence of oolite shoals, could reflect either the absence of algae to stabilize platform-margin sediments and to provide a substrate for microbial communities or the failure of such organisms to lithify rapidly. If present, what factors could have prevented algae on the platform margin from being associated with penecontemporaneous micritic cements? The consistent deposition of micritic cement around an alga to form *Tubiphytes* suggests that the alga itself provided a substrate for a microbial community. One specific hypothesis—testable but not

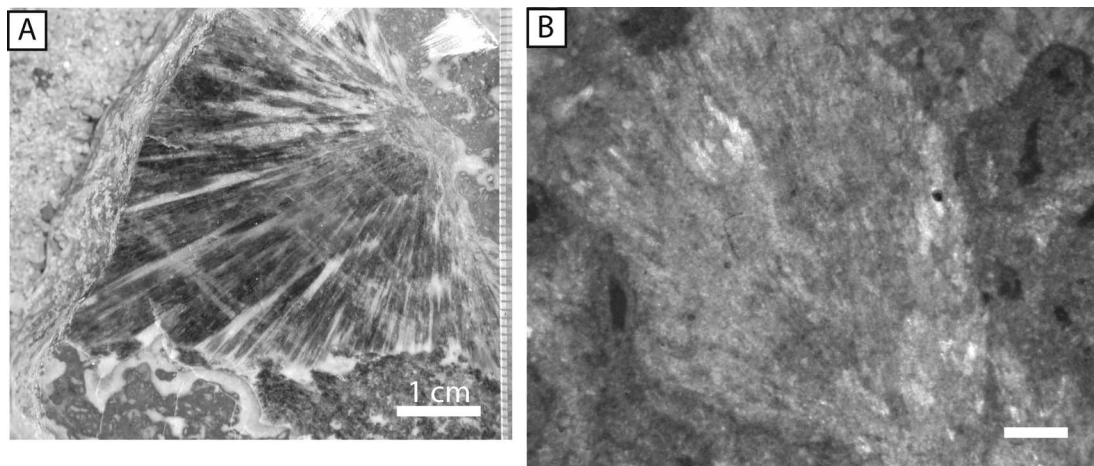


FIGURE 16—Botryoidal cements; scale bar=1 mm. (A) Slab photo of a large botryoid (Reef 10–24). (B) Photomicrograph of a botryoid (Reef 7–17).

necessarily exclusive—is a change in the importance of photorespiration for algae from the Early to the Middle Triassic. Under high photorespiratory stress, many green algae excrete glycolate as a metabolic waste product (Stabenau and Winkler, 2005), which could have then served as a substrate for microbial communities. Photorespiratory stress is enhanced when the ratio of CO_2/O_2 is low. Lithological observations (Retallack, 1999; Wignall and Twitchett, 2002) and geochemical models (e.g., Berner and Kothavala, 2001) suggest an increase in the CO_2/O_2 ratio from the Permian to the Early Triassic and a decrease in the ratio from the Early to the Middle Triassic. If the trends suggested by these observations are correct, an increase in the rate of glycolate secretion among soft-bodied algae during the Middle Triassic could account for the stabilization of the platform-margin substrate by favoring the formation of a heavily cemented reef margin in the place of oolite shoals.

Regardless of the precise scenario responsible for the initiation of *Tubiphytes* reefs early in the Anisian, the transition on the GBG from oolite shoals containing giant ooids to a heavily cemented *Tubiphytes*-reef complex in the Anisian constrains explanations for the absence of Early Triassic reefs. In contrast to speculation that carbonate sedimentation was significantly stalled by the absence of reefs in the Early Triassic (e.g., Flügel and Stanley, 1984), all evidence indicates that the rate of carbonate precipitation was relatively rapid during the Early Triassic. For example, Lower Triassic carbonate sections in the Nanpanjiang Basin reach up to 900 m in thickness, indicating robust carbonate accumulation rates within the basin (Koenig et al., 2001). Therefore, interpretations of the absence of reefs and reef-building metazoans in the Early Triassic as a reflection of oceanographic conditions unfavorable to carbonate deposition (e.g., Flügel and Stanley, 1984; Stanley, 1988) are not supported, although brief episodes unfavorable to carbonate deposition, as could be created by the rapid introduction of large volumes of CO_2 to the atmosphere, cannot be ruled out.

The absence of reef-building metazoans and calcareous algae from the Lower Triassic rock record may be explained by one of the same two types of explanation that could account for the absence of *Tubiphytes*: a

lack of potentially stabilizing or framework-building organisms, or a failure of such organisms to calcify. The former scenario is suggested by the fact that calcareous sponges, calcareous algae, and other reef-dwelling and reef-building organisms typically occur in the same environments that are preserved in the Lower Triassic rock record, namely shallow, tropical, carbonate ramps and banks. The lack of obvious, detailed taxonomic affinities between Permian and Triassic calcareous sponges (Flügel, 2002) is at least compatible with a scenario involving the extinction of calcifying lineages followed by the acquisition of calcification in previously non-calcifying lineages, although more work is needed to test this possibility. On the other hand, environmental conditions can interfere with the ability of calcifying organisms to secrete their skeletons. As discussed above, it seems unlikely that precipitation of calcium carbonate could be inhibited in the tropical surface ocean for long intervals during the Early Triassic. However, temperature, or interactive effects between temperature and P_{CO_2} , may affect biologically controlled calcification independent of the carbonate saturation state. A detrimental effect of high temperature—independent of P_{CO_2} —is suggested by experiments and field observations (e.g., Reynaud et al., 2003; Carricart-Ganivet, 2004; Marshall and Clode, 2004). The generality of this finding is not yet clear because earlier studies (e.g., Gattuso et al., 1998; Langdon et al., 2000; Leclercq et al., 2000) primarily focused on the role of saturation state and P_{CO_2} on calcification, and at least one study (McNeil et al., 2004) has found a positive effect of temperature on calcification rate in modern corals.

If temperature does have physiological effects on calcification, and if excessively high temperatures have adverse effects on calcification, then the absence of heavily calcified, reef-building metazoans through the Early Triassic may be, in part, a consequence of persistent greenhouse conditions (Retallack, 1999). If so, temperatures in the tropics during the Early Triassic must have been even warmer than during other warm intervals of extensive reef development, such as the Devonian. It is suggestive that one of two reports of Early Triassic calcareous algae comes from Spitsbergen (Wignall et al., 1998), which was situated at relatively

TABLE 2—Timing and inferred original mineralogy of deposition of cement phases within the reef complex.

Cement phase	Timing	Mineralogy
<i>Tubiphytes micritic envelope</i>	Penecontemporaneous	Mg calcite?
Peloidal micritic cement	Penecontemporaneous	Mg calcite
Brown fibrous cement	Penecontemporaneous	Aragonite or high-Mg calcite
Isopachous fibrous cement	Early diagenesis	Aragonite or high-Mg calcite
Botryoidal cement	Early diagenesis	Aragonite
Sparry calcite	Later diagenesis	Calcite

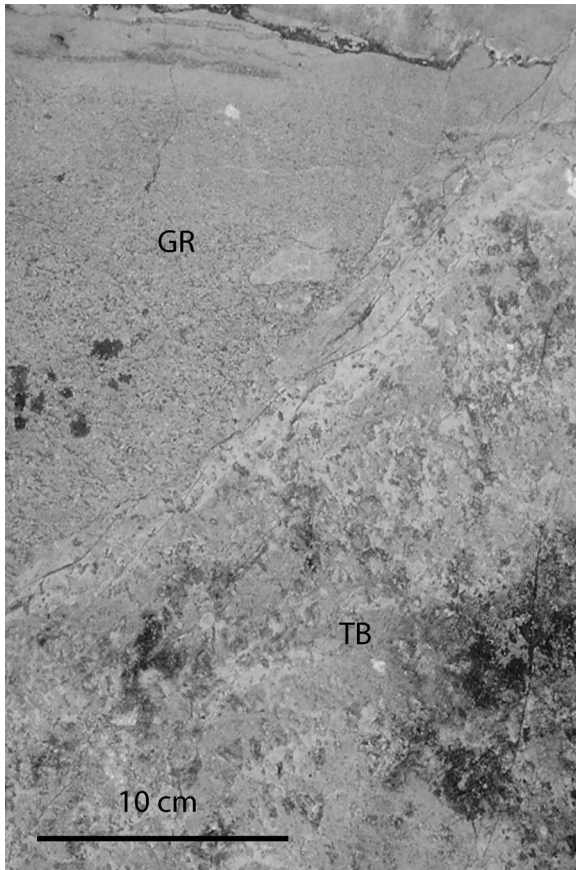


FIGURE 17—Local relief of *Tubiphytes* boundstone (TB) shown against overlapping *Tubiphytes* grainstone (GR); note graded bedding within the grainstone.

high northern latitudes at the time, because a predicted consequence of greenhouse climate would be more rapid recovery at high latitudes and the migration of tropical faunas to higher latitudes. Greenhouse climate, through its effects on animal and bacterial respiration rates, also may have played a central role in limiting the abundance of skeletal and, perhaps, soft-bodied animals in Early Triassic oceans (Payne et al., 2006). The absence of heavily calcified, reef-building animals and algae may reflect the same controls, enhanced by the additional inhibition of biotic calcification by high temperature. Such an effect would be particularly pronounced if the combination of temperature regime and carbonate saturation state required by heavily calcified organisms was not met anywhere in Early Triassic oceans because, for example, the tropics were too hot while higher-latitude oceans were not sufficiently saturated with calcium carbonate to facilitate heavy calcification. The absence of micritic cements around soft-bodied algae to form *Tubiphytes*-like frameworks is more problematic, and may result from either the low abundance of Early Triassic soft-bodied algae, the effects of high Early Triassic P_{CO_2} on algal physiology, or both.

CONCLUSIONS

The Anisian reef complex on the Great Bank of Guizhou is the oldest-known Middle Triassic reef and it also is exceptionally well preserved. Initiation of the reef late in the Spathian is indicated by the occurrence of distinctive grains within carbonate turbidites on the basin margin before the biostratigraphic Early–Middle Triassic boundary. Unlike its better-studied European counterparts, the reef margin has not been dolomitized and, furthermore, a platform-to-basin cross section of the reef complex has been exposed on the limb of a faulted syncline, facilitating investigation. The reef complex consists of boundstones and grainstones. Boundstone framework primarily consists of *Tubiphytes*, a structure that appears to have formed when micritic cement precipitated within a bacterial mat living in association with soft-bodied algae. Most of the volume of the boundstone facies consists of several generations of early-marine cement: clotted micritic cement, brown-fibrous cement, botryoidal cement, and isopachous-fibrous cement. In some cases, isopachous-fibrous cement fills dissolution cavities and may have formed during early burial. Boundstone facies contain a low-diversity biota of bivalves, gastropods, brachiopods, crinoids, ostracodes, and foraminifera, as well as rare

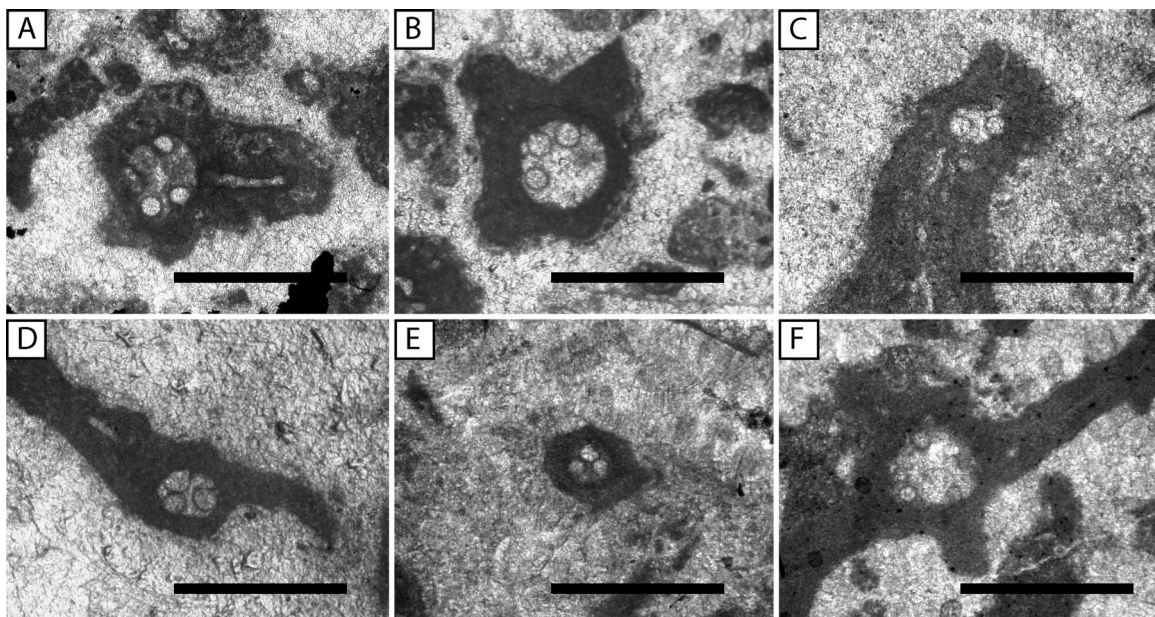


FIGURE 18—*Tubiphytes* reproductive structures, illustrating the presence of small spore-like structures (~50–75 μm diameter) contained within larger spherules (~500 μm diameter) interpreted as algal sporangia; scale bars=1 mm. (A) Sample R-227. (B) Sample PUG-15. (C) Sample R-3. (D) Sample R-74. (E) Sample Reef 4–8. (F) Sample Reef 8–18.

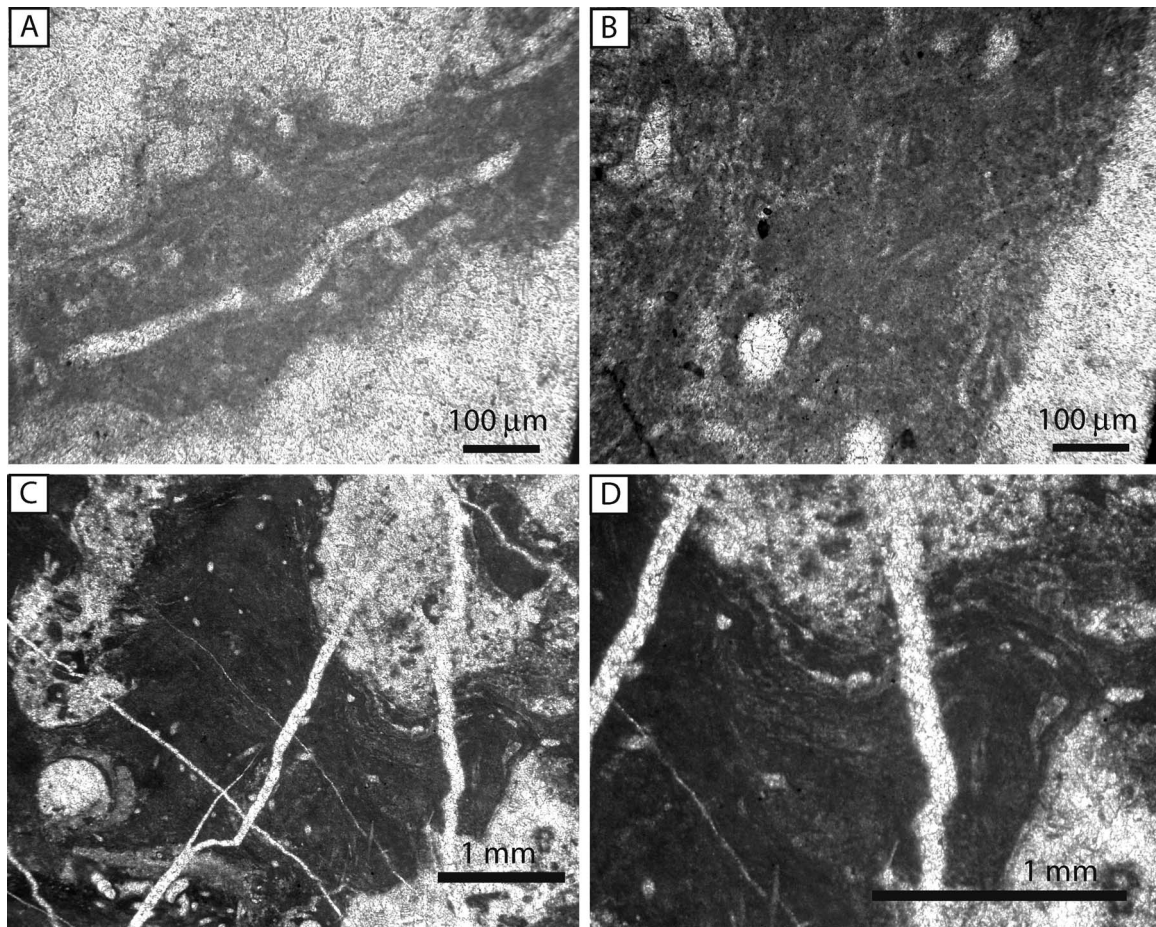


FIGURE 19—Photomicrographs showing microbial structures within micrite on *Tubiphytes* in sample R-93. (A) Filaments within *Tubiphytes* micrite. (B) Filaments within *Tubiphytes* micrite. (C) Stromatolitic laminae within *Tubiphytes* micrite. (D) Detail of C.

sponges and corals in the youngest parts of the reef. Grainstones contain the same suite of fossil grains observed within the boundstone facies, and are dominated by *Tubiphytes*. The limited role of metazoans and calcareous algae as framework builders or even as sources of carbonate sediment suggests that the principal role of biotic recovery from the end-Permian extinction in reef formation was sediment stabilization along the platform margin. Stabilization of the sediment by algae and associated microbial mats facilitated carbonate precipitation along the platform margin in the form of micritic, fibrous, and botryoidal cements, rather than as ooids. Only later in the Triassic did the evolution and diversification of scleractinian corals, calcareous sponges, and calcareous algae result in the development of reefs quantitatively dominated by skeletal metazoans. Explaining the absence of platform-margin reefs from the Lower Triassic rock record requires identifying factors that could inhibit the formation of a cemented *Tubiphytes* framework on a global scale for several million years.

ACKNOWLEDGMENTS

We thank R. Bambach, W. Fischer, C. Marshall, S. Pruss, and D. Schrag for helpful discussions and comments on the manuscript, and H. Yao, Y. Yu, J. Xiao, A. Bush, and R. Kodner for assistance in the field. This work was funded by the Petroleum Research Fund of the American Chemical Society (ACS-PRF 40948-B2 to DJL), the National Science Foundation (EAR-9804835 to DJL and OCE-0084032 to AHK—Project EREUPT), Sigma Xi (Grant-in-Aid of Research to JLP) and the Department of Defense (National Defense Science and Engineering Graduate Fellowship to JLP).

REFERENCES

- BACHMANN, G.H., 1979, Bioherme der Muschel *Placunopsis ostracina* v. Schlotheim und ihre Diagenese: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 158, p. 381–407.
- BACHMANN, G.H., 2002, A lamellibranch-stromatolite bioherm in the Lower Keuper (Ladinian, Middle Triassic), south Germany: Facies, v. 46, p. 83–88.
- BAUD, A., CIRILLI, S., and MARCOUX, J., 1997, Biotic response to mass extinction: the lowermost Triassic microbialites: Facies, v. 36, p. 238–242.
- BERNER, R.A., and KOTHAVALA, Z., 2001, GEOCARB III: a revised model of atmospheric CO₂ over Phanerozoic time: American Journal of Science, v. 301, p. 182–204.
- BLENDINGER, W., 1983, Anisian sedimentation and tectonics of the M. Pore-M. Cernera area (Dolomites): Rivista Italiana di Paleontologia e Stratigrafia, v. 89, p. 175–208.
- BOWRING, S.A., ERWIN, D.H., JIN, Y.G., MARTIN, M.W., DAVIDEK, K., and WANG, W., 1998, U/Pb zircon geochronology and tempo of the end-Permian mass extinction: Science, v. 280, p. 1039–1045.
- BROGLIO LORIGA, C., MASETTI, D., and NERI, C., 1982, La formazione di Werfen (Scitico) delle Dolomiti Occidentali; sedimentologia biostratigrafia: Rivista Italiana Di Paleontologia E Stratigrafia, v. 88, p. 501–598.
- CARRICART-GANIVET, J.P., 2004, Sea surface temperature and the growth of the West Atlantic reef-building coral *Montastraea annularis*: Journal of Experimental Marine Biology and Ecology, v. 302, p. 249–260.
- CHRISTENSEN, S., and LEHRMANN, D.J., 2004, Distribution, composition, and paleoecology of Middle Triassic carbonate reefs of the Nanpanjiang Basin, Guizhou, Guangxi, and Yunnan, South China: Geological Society of America, North Central Section, Abstracts with Program, v. 36, p. 10.
- COPPER, P., 2001, Reefs during the multiple crises towards the Ordovician-Silurian boundary: Anticosti Island, eastern Canada, and worldwide: Canadian Journal of Earth Sciences, v. 38, p. 153–171.

- COPPER, P., 2002, Reef development at the Frasnian/Famennian mass extinction boundary: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 181, p. 27–65.
- ENKIN, R.J., YANG, Z.Y., CHEN, Y., and COURTILOTT, V., 1992, Paleomagnetic constraints on the geodynamic history of the major blocks of China from the Permian to the present: *Journal of Geophysical Research, Solid Earth*, v. 97, p. 13953–13989.
- ENOS, P., WEI, J.Y., and LEHRMANN, D.J., 1998, Death in Guizhou—Late Triassic drowning of the Yangtze carbonate platform: *Sedimentary Geology*, v. 118, p. 55–76.
- ENOS, P., WEI, J.Y., and YAN, Y.J., 1997, Facies distribution and retreat of Middle Triassic platform margin, Guizhou Province, South China: *Sedimentology*, v. 44, p. 563–584.
- EZAKI, Y., LIU, J.B., and ADACHI, N., 2003, Earliest Triassic microbialite micro- to megastructures in the Huaying area of Sichuan Province, South China: implications for the nature of oceanic conditions after the end-Permian extinction: *PALAIOS*, v. 18, p. 388–402.
- FAGERSTROM, J.A., and WEIDLICH, O., 1999, Strengths and weaknesses of the reef guild concept and quantitative data: application to the upper Capitan massive community (Permian), Guadalupe Mountains, New Mexico–Texas: *Facies*, v. 40, p. 131–156.
- FLÜGEL, E., 1982, *Microfacies Analysis of Limestones*: Springer, New York, 633 p.
- FLÜGEL, E., 1994, Pangean shelf carbonates: controls and paleoclimatic significance of Permian and Triassic reefs: in Klein, G.D., ed., *Pangea: Paleoclimate, Tectonics and Sedimentation during Accretion, Zenith, and Breakup of a Supercontinent*: Geological Society of America Special Publication 288, p. 247–266.
- FLÜGEL, E., 2002, Triassic reef patterns: in Kiessling, W., Flügel, E., and Golonka, J., eds., *Phanerozoic Reef Patterns*: SEPM Special Publication 72, Society for Sedimentary Geology, Tulsa, p. 391–464.
- FLÜGEL, E., 2004, *Microfacies of Carbonate Rocks*: Springer, Berlin, 976 p.
- FLÜGEL, E., and STANLEY, G.D., 1984, Reorganization, development and evolution of post-Permian reefs and reef organisms: *Palaeontographica Americana*, v. 54, p. 177–186.
- GAETANI, M., and GORZA, M., 1989, The Anisian (Middle Triassic) carbonate bank of Camorelli (Lombardy, southern Alps): *Facies*, v. 21, p. 41–56.
- GATTUSO, J.P., FRANKIGNOULLE, M., BOURGE, I., ROMAINE, S., and BUDDEMEIER, R.W., 1998, Effect of calcium carbonate saturation of seawater on coral calcification: *Global and Planetary Change*, v. 18, p. 37–46.
- GROTZINGER, J.P., and KNOLL, A.H., 1995, Anomalous carbonate precipitates: is the Precambrian the key to the Permian?: *PALAIOS*, v. 10, p. 578–596.
- GROVES, J.R., and CALNER, M., 2004, Lower Triassic oolites in Tethys: a sedimentologic response to the end-Permian mass extinction: *Geological Society of America, Annual Meeting, Abstracts with Program*, v. 36, p. 336.
- HAGDORN, H., 1982, The “Bank der kleinen Terebrateln” (Upper Muschelkalk, Triassic) near Schwäbisch Hall (SW-Germany)—a tempestite condensation horizon: in Einsele, G., and Seilacher, A., eds., *Cyclic and Event Stratification*: Springer, New York, p. 263–285.
- HARRIS, M.T., 1993, Reef fabrics, biotic crusts and syndepositional cements of the Latemar reef margin (Middle Triassic), Northern Italy: *Sedimentology*, v. 40, p. 383–401.
- HEYDARI, E., HASSANZADEH, J., WADE, W.J., and GHAZI, A.M., 2003, Permian-Triassic boundary interval in the Abadeh section of Iran with implications for mass extinction: Part 1—sedimentology: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 193, p. 405–423.
- KEIM, L., and SCHLAGER, W., 2001, Quantitative compositional analysis of a Triassic carbonate platform (Southern Alps, Italy): *Sedimentary Geology*, v. 139, p. 261–283.
- KERSHAW, S., GUO, L., SWIFT, A., and FAN, J.S., 2002, Microbialites in the Permian-Triassic boundary interval in Central China: structure, age and distribution: *Facies*, v. 47, p. 83–89.
- KIESSLING, W., 2005, Long-term relationships between ecological stability and biodiversity in Phanerozoic reefs: *Nature*, v. 433, p. 410–413.
- KNOLL, A.H., and SWETT, K., 1990, Carbonate deposition during the Late Proterozoic Era—an example from Spitsbergen: *American Journal of Science*, v. 290A, p. 104–132.
- KOENIG, J., DILLET, P., LEHRMANN, D.J., and ENOS, P., 2001, Structural and paleogeographic elements of the Nanpanjiang Basin, Guizhou, Guangxi, and Yunnan provinces, South China: a compilation from satellite images, regional geologic maps and ground observations: *American Association of Petroleum Geologists, Annual Meeting, Abstracts with Program*, v. 10, p. A107.
- LANGDON, C., TAKAHASHI, T., SWEENEY, C., CHIPMAN, D., GODDARD, J., MARUBINI, F., ACEVES, H., BARNETT, H., and ATKINSON, M.J., 2000, Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef: *Global Biogeochemical Cycles*, v. 14, p. 639–654.
- LECLERCQ, N., GATTUSO, J.P., and JAUBERT, J., 2000, CO₂ partial pressure controls the calcification rate of a coral community: *Global Change Biology*, v. 6, p. 329–334.
- LEHRMANN, D.J., 1993, *Sedimentary geology of the Great Bank of Guizhou: birth, evolution and death of a Triassic isolated carbonate platform, Guizhou Province, South China*: Unpublished PhD dissertation, University of Kansas, Lawrence, 457 p.
- LEHRMANN, D.J., 1999, Early Triassic calcimicrobial mounds and biostromes of the Nanpanjiang basin, South China: *Geology*, v. 27, p. 359–362.
- LEHRMANN, D.J., PAYNE, J.L., FELIX, S.V., DILLET, P.M., WANG, H., YU, Y.Y., and WEI, J.Y., 2003, Permian-Triassic boundary sections from shallow-marine carbonate platforms of the Nanpanjiang Basin, South China: implications for oceanic conditions associated with the end-Permian extinction and its aftermath: *PALAIOS*, v. 18, p. 138–152.
- LEHRMANN, D.J., WAN, Y., WEI, J.Y., YU, Y.Y., and XIAO, J.F., 2001, Lower Triassic peritidal cyclic limestone: an example of anachronistic carbonate facies from the Great Bank of Guizhou, Nanpanjiang Basin, Guizhou Province, South China: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 173, p. 103–123.
- LEHRMANN, D.J., WEI, J.Y., and ENOS, P., 1998, Controls on facies architecture of a large Triassic carbonate platform: the Great Bank of Guizhou, Nanpanjiang Basin, South China: *Journal of Sedimentary Research*, v. 68, p. 311–326.
- MARSHALL, A.T., and CLODE, P., 2004, Calcification rate and the effect of temperature in a zooxanthellate and an azooxanthellate scleractinian reef coral: *Coral Reefs*, v. 23, p. 218–224.
- MCNEIL, B.I., MATEAR, R.J., and BARNES, D.J., 2004, Coral reef calcification and climate change: the effect of ocean warming: *Geophysical Research Letters*, v. 31, p. L22309.
- MELLO, J., 1977, *Plexoramea cerebriformis* n. gen. n. sp. and some other microproblems and microfossils from Triassic limestones of the West Carpathians: *Západné Karpaty, Séria, Paleotológia*, v. 2–3, p. 189–202.
- MUNDIL, R., BRACK, P., MEIER, M., RIEBER, H., and OBERLI, F., 1996, High resolution U-Pb dating of Middle Triassic volcanics: time-scale calibration and verification of tuning parameters for carbonate sedimentation: *Earth and Planetary Science Letters*, v. 141, p. 137–151.
- MUNDIL, R., LUDWIG, K.R., METCALFE, I., and RENNE, P.R., 2004, Age and timing of the Permian mass extinctions: U/Pb dating of closed-system zircons: *Science*, v. 305, p. 1760–1763.
- MUTTONI, G., NICORA, A., BRACK, P., and KENT, D.V., 2004, Integrated Anisian-Ladinian boundary chronology: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 208, p. 85–102.
- OGG, J., 2004, Overview of global boundary stratotype sections and points (GSSP's): International Commission on Stratigraphy, <<http://www.stratigraphy.org>> [checked 4–14–06]
- PAYNE, J.L., LEHRMANN, D.J., WEI, J., and KNOLL, A.H., 2006, The pattern and timing of biotic recovery from the end-Permian extinction on the Great Bank of Guizhou, Guizhou Province, China: *PALAIOS*, v. 21, p. 63–85.
- PAYNE, J.L., LEHRMANN, D.J., WEI, J.Y., ORCHARD, M.J., SCHRAG, D.P., and KNOLL, A.H., 2004, Large perturbations of the carbon cycle during recovery from the end-Permian extinction: *Science*, v. 305, p. 506–509.
- PFEIFFER, J., 1988, Paleontology and microfacies of a platform margin in the Carnic Alps (Austria, Middle Triassic): *Facies*, v. 19, p. 33–60.
- PRUSS, S.B., and BOTTIER, D.J., 2004, Late Early Triassic microbial reefs of the Western United States: a description and model for their deposition in the aftermath of the end-Permian mass extinction: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 211, p. 127–137.
- PUGLIESE, A., 1997, Middle-Late Triassic dasycladales (green algae) from Brenta Dolomites (Gudicarie Alps, Italy): *Rivista Italiana di Paleontologia e Stratigrafia*, v. 103, p. 71–80.
- RESTALLACK, G.J., 1999, Postapocalyptic greenhouse paleoclimate revealed by earliest Triassic paleosols in the Sydney Basin, Australia: *Geological Society of America Bulletin*, v. 111, p. 52–70.
- REYNAUD, S., LECLERCQ, N., ROMAINE-LIQUID, S., FERRIER-PAGES, C., JAUBERT, J., and GATTUSO, J.P., 2003, Interacting effects of CO₂ partial pressure and temperature on photosynthesis and calcification in a scleractinian coral: *Global Change Biology*, v. 9, p. 1660–1668.
- RIDGWELL, A.J., 2005, A mid-Mesozoic revolution in the regulation of ocean chemistry: *Marine Geology*, v. 217, p. 339–357.
- RIDING, R., and GUO, L., 1992, Affinities of *Tubiphytes*: *Palaeontology*, v. 35, p. 37–49.
- RUSSO, F., MASTANDREA, A., STEFANI, M., and NERI, C., 2000, Carbonate facies dominated by syndepositional cements: a key component of Middle Triassic platforms. The Marmolada case history (Dolomites, Italy): *Facies*, v. 42, p. 211–226.
- RUSSO, F., NERI, C., MASTANDREA, A., and BARACCA, A., 1997, The mud mound nature of the Cassian platform margins of the Dolomites. A case history: the Cipit boulders from Punta Grohmann (Sasso Piatto Massif, Northern Italy): *Facies*, v. 36, p. 25–36.
- SANO, H., and NAKASHIMA, K., 1997, Lowermost Triassic (Griesbachian) microbial bindstone-cementstone facies, southwest Japan: *Facies*, v. 36, p. 1–24.
- SCHOLZ, G., 1972, An Anisian Wetterstein limestone reef in North Hungary: *Acta Mineralogica-Petrographica, Szeged*, v. 20, p. 337–362.

- SCHUBERT, J.K., and BOTTJER, D.J., 1992, Early Triassic stromatolites as post mass extinction disaster forms: *Geology*, v. 20, p. 883–886.
- SEELING, M., EMMERICH, A., BECHSTADT, T., and ZUHLKE, R., 2005, Accommodation/sedimentation development and massive early marine cementation: Latemar vs. Concarena (Middle/Upper Triassic, Southern Alps): *Sedimentary Geology*, v. 175, p. 439–457.
- SENOWBARI-DARYAN, B., and FLÜGEL, E., 1993, *Tubiphytes* Maslov, an enigmatic fossil: classification, fossil record and significance through time, part I: discussion of Late Paleozoic material: in Barattolo, F., De Castro, P., and Parente, M., eds., *Studies on Fossil Benthic Algae: Bolletino della Societa Paleontologica Italiana, Volume Speciale 1*, p. 353–382.
- SENOWBARI-DARYAN, B., ZÜHLKE, R., BECHSTADT, T., and FLÜGEL, E., 1993, Anisian (Middle Triassic) buildups of the Northern Dolomites (Italy); the recovery of reef communities after the Permian/Triassic crisis: *Facies*, v. 28, p. 181–256.
- SHEN, J.W., and WEBB, G.E., 2004, Famennian (Upper Devonian) calcimicrobial (*Renalcis*) reef at Miaomen, Guilin, Guangxi, South China: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 204, p. 373–394.
- SEWERS, F.D., 2003, Oolite and coated grains: in Middleton, G.V., ed., *Encyclopedia of Sedimentology*: Kluwer, Boston, p. 66–70.
- STABENAU, H., and WINKLER, U., 2005, Glycolate metabolism in green algae: *Physiologia Plantarum*, v. 123, p. 235–245.
- STANLEY, G.D., 1988, The history of early Mesozoic reef communities: a three-step process: *PALAIOS*, v. 3, p. 170–183.
- SUMNER, D.Y., and GROTZINGER, J.P., 1993, Numerical modeling of ooid size and the problem of Neoproterozoic giant ooids: *Journal of Sedimentary Petrology*, v. 63, p. 974–982.
- SWETT, K., and KNOLL, A.H., 1989, Marine pisolites from Upper Proterozoic carbonates of East Greenland and Spitsbergen: *Sedimentology*, v. 36, p. 75–93.
- SZULC, J., 2000, Middle Triassic evolution of the northern Peri-Tethys area as influenced by early opening of the Tethys Ocean: *Annales Societatis Geologorum Poloniae*, v. 70, p. 1–47.
- VACHARD, D., HAUSER, M., MARTINI, R., ZANINETTI, L., MATTER, A., and PETERS, T., 2001, New algae and problematica of algal affinity from the Permian of the Aseelah unit of the Batain Plain (east Oman): *Geobios*, v. 34, p. 375–404.
- WANG, S.-H., FAN, J.-S., and RIGBY, J.K., 1994, *Archaeolithoporella* and *Tubiphytes*: affinities and paleoecology in Permian reefs of South China: *Science in China, Series B*, v. 37, p. 723–743.
- WEBB, G.E., 1998, Earliest known Carboniferous shallow-water reefs, Gudman Formation (Tn1b), Queensland, Australia: implications for Late Devonian reef collapse and recovery: *Geology*, v. 26, p. 951–954.
- WEIDLICH, O., 2005, PTB mass extinction and earliest Triassic recovery overlooked? A reinterpretation of earliest Triassic microbial carbonates of the Central European Basin (Germany): *Albertiana*, v. 33, p. 89–90.
- WIGNALL, P.B., MORANTE, R., and NEWTON, R., 1998, The Permo-Triassic transition in Spitsbergen: $^{13}\text{C}_{\text{org}}$ chemostratigraphy, Fe and S geochemistry, facies, fauna and trace fossils: *Geological Magazine*, v. 135, p. 47–62.
- WIGNALL, P.B., and TWITCHETT, R.J., 2002, Extent, duration, and nature of the Permian–Triassic superanoxic event: in Koeberl, C., and MacLeod, K.G., eds., *Catastrophic Events and Mass Extinctions: Impacts and Beyond*: Geological Society of America Special Paper 356, p. 395–413.
- WOOD, R., 1998, Novel reef fabrics from the Devonian Canning Basin, Western Australia: *Sedimentary Geology*, v. 121, p. 149–156.
- WOODS, A.D., BOTTJER, D.J., MUTTI, M., and MORRISON, J., 1999, Lower Triassic large sea-floor carbonate cements: their origin and a mechanism for the prolonged biotic recovery from the end-Permian mass extinction: *Geology*, v. 27, p. 645–648.
- YANG, W., and LEHRMANN, D.J., 2003, Milankovitch climatic signals in Lower Triassic (Olenekian) peritidal carbonate successions, Nanpanjiang Basin, South China: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 201, p. 283–306.

ACCEPTED JANUARY 6, 2006

