

Paleoecology and geochemistry of Early Triassic (Spathian) microbial mounds and implications for anoxia following the end-Permian mass extinction

Pedro J. Marenco^{1*}, Julie M. Griffin¹, Margaret L. Fraiser^{2*}, and Matthew E. Clapham^{3*}

¹Department of Geology, Bryn Mawr College, Bryn Mawr, Pennsylvania 19010, USA

²Department of Geosciences, University of Wisconsin–Milwaukee, Milwaukee, Wisconsin 53201, USA

³Department of Earth and Planetary Sciences, University of California–Santa Cruz, Santa Cruz, California 95064, USA

ABSTRACT

Large microbialite mounds (1–2 m in height) have previously been reported from two units within the Spathian section of the Virgin Limestone Member of the Moenkopi Formation at Lost Cabin Spring, Nevada (United States). Previous investigations led to the interpretation that the mounds were formed under anoxic and alkaline conditions that suppressed metazoan grazers and delayed the biotic recovery from the end-Permian mass extinction. Here we report low organic carbon and total sulfur abundances throughout the section that suggest that anoxia was not prevalent during deposition. We also report that the upper mound-bearing unit contains stromatolite-sponge patch reefs in which mutual encrustation between stromatolites and sponges contributed to the building of a reef framework. The stromatolite-sponge patch reefs contain discrete burrows within stromatolitic laminations, suggesting that there was sufficient oxygen for grazing during the formation of the upper unit mounds. The enhanced ecological complexity of the upper unit mounds leads us to conclude that the mounds represent the transition to biotic recovery following the end-Permian mass extinction.

INTRODUCTION

Early Triassic rocks provide a glimpse into the aftermath of the end-Permian mass extinction, the most devastating extinction of the Phanerozoic (e.g., Erwin, 1993; Payne and Clapham, 2012). Although the cause of the mass extinction is still debated, some combination of volcanism, climate warming, high atmospheric carbon dioxide, and ocean anoxia or euxinia likely played a role in the mass extinction, and possibly in the delayed biotic recovery (e.g., Kamo et al., 2003; Nielsen and Shen, 2004; Grice et al., 2005; Kump et al., 2005; Riccardi et al., 2006; Fraiser and Bottjer, 2007; Knoll et al., 2007). Although biotic recovery may have begun sooner in some regions (e.g., Krystyn et al., 2003; Twitchett et al., 2004), and in some taxa (e.g., Orchard, 2007; Baud et al., 2008; Brayard et al., 2009; Brayard et al., 2011), the vast majority of Early Triassic successions in eastern Panthalassa and Tethys contain low-diversity benthic invertebrate faunas for an interval of ~5 m.y. (Erwin, 1993; Mundil et al., 2004; Lehrmann et al., 2006). In addition to low-diversity faunas and geochemical anomalies (Holser, 1984; Payne et al., 2004; Corsetti et al., 2005; Marenco et al., 2008), subtidal stromatolites and other microbialites have been reported from Early Triassic rocks around the world (e.g., Kershaw et al., 1999; Pruss and Bottjer, 2004; Baud et al., 2005). It has been suggested that Early Triassic microbialites indicate anomalous environmental conditions because modern microbialites tend to form in environments that are inhospitable to metazoans (Pruss and Bottjer, 2004).

Stromatolite buildups (1–2 m in height) have been reported from the Spathian Virgin Limestone Member of the Moenkopi Formation (herein referred to as the Virgin Limestone) at Lost Cabin Spring, Nevada (United States) (Schubert and Bottjer, 1992). Although other microbialite units exist within the Virgin Limestone (Pruss and Payne, 2009; Mata and Bot-

tjer, 2011), two units have received the most attention because of the size of the microbialite buildups (Schubert and Bottjer, 1992; Pruss and Bottjer, 2004). Schubert and Bottjer (1992) first described the microbialite mounds from the two stromatolite beds as “disaster taxa” (but see Kershaw et al., 2009) that exploited the absence of metazoan grazers following the end-Permian mass extinction. Pruss and Bottjer (2004) argued that the lower stromatolite unit at Lost Cabin Spring was a set of patch-reef mounds that grew between fairweather and storm wave base. The stromatolite patch reefs were hypothesized to have developed in part because of incursions of anoxic, alkaline deep water that suppressed grazing and bioturbating organisms that would otherwise have fed upon, and prevented the buildup of, microbial mats (Pruss and Bottjer, 2004).

The Lost Cabin Spring stromatolites have been linked with Early Triassic aragonite fans, flat pebble conglomerates, and other microbialites, suggesting that these features represent deleterious and unusual marine conditions (Pruss et al., 2006; Baud et al., 2007; Woods, 2009). Mata and Bottjer (2011) studied the Virgin Limestone microbialites and concluded that the buildups grew on hardgrounds precipitated from the upwelling of carbonate-saturated, low-oxygen water.

Here we report the results of our spatial, petrographic, and geochemical investigations of the two stromatolite mound-bearing units at Lost Cabin Spring. Our investigation revealed that the buildups of the upper unit are actually stromatolite-sponge framework patch reefs and that anoxia was likely not a factor in the formation of the mounds in either unit. The metazoan-microbe patch reefs reported here are the largest and most ecologically complex of those reported from Early Triassic rocks.

GEOLOGIC SETTING

The Virgin Limestone consists of a westward-thickening wedge of interbedded carbonates and siliciclastics deposited over present-day southern Nevada, northern Arizona, and southern Utah (McKee, 1954; Poborski, 1954). The depositional environments of the Virgin Limestone range from supratidal to middle shelf, suggesting that the member represents a gently west dipping, distally steepening carbonate ramp that deepened into the low-latitude eastern Panthalassa Ocean (Blakey, 1974). Lost Cabin Spring is located in the Spring Mountains, east of Pahrump, Nevada (base of section near 36°05'00.0"N, 115°39'13.3"W). The locality is Spathian in age, based on the presence of the ammonite *Tirolites* (Poborski, 1954) found within marine siltstones of the correlative Virgin Limestone near St. George, Utah. In addition, the strontium isotopic record (see Marenco et al., 2008) on limestones from Beyond Lost Cabin, a locality 3 km southeast of Lost Cabin Spring, can be matched to the strontium isotope profile for the Spathian (Korte et al., 2003).

METHODS

We systematically collected samples for geochemistry and petrography at a resolution of ~10 m using a Jacob staff fitted with a Topographic Abney level for precise stratigraphic measurement. Additional field measurements were made within each of the two mound-bearing units (at ~95 m and 155 m height in the section; see Fig. 1) in order to document the internal structure of mounds. In this paper, “mound” refers to a group of

*E-mails: pmarenco@brynmawr.edu; mfraiser@uwm.edu; mclapham@ucsc.edu.

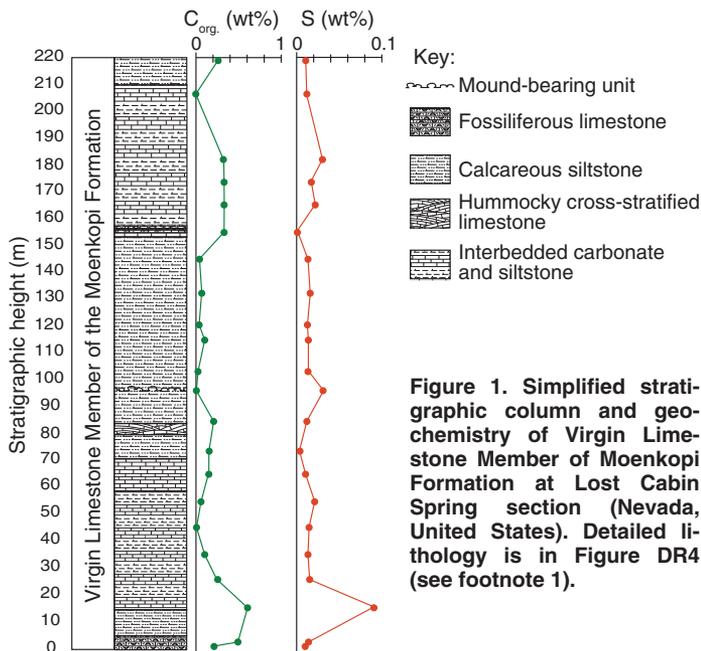


Figure 2. Outcrop photograph of stromatolite-sponge mound of upper mound-bearing unit at Lost Cabin Spring (Nevada, United States). Scale bar at left is 1 m. Dashed line delineates mound from underlying crinoidal grainstone. Black box is area of magnification in Figure 3.

smaller individual microbial buildups that coalesce with increased height, becoming laterally linked; as used herein, mounds are macroscopic structures that can be seen beyond a few meters from the outcrop.

Samples were cut into billets, made into thin (30 μm) and thick (60 μm) sections, by Burnham Petrographics LLC (Idaho), and observed with a petrographic microscope. A second subset of the samples was powdered for geochemical analysis. An Eltra carbon and sulfur determinator equipped with a total inorganic carbon (TIC) module was used to determine the weight percent total carbon, total sulfur, and inorganic carbon for each sample by ultraviolet attenuation. For total sulfur and total carbon measurements, ~150 mg of powdered sample was combusted at 1350 $^{\circ}\text{C}$. Replicate analyses of samples and standards yielded results within 0.02 wt% for total sulfur and 0.1 wt% for total carbon. Approximately 50 mg of powdered sample was dissolved in 40% HCl under constant heat and agitation for measurement of TIC content as CO_2 . Replicate analyses of TIC on standards were reproducible to within 0.1 wt%. Organic carbon content was calculated by taking the difference of the total carbon and TIC weight percent values.

RESULTS

The samples from Lost Cabin Spring contain an average of 0.2 wt% organic carbon and 0.02 wt% total sulfur (Fig. 1). Total sulfur values are assumed to reflect pyrite content, given the lack of sulfate-bearing minerals revealed in our petrographic analysis. Neither of the two mound-bearing units is exceptional in terms of organic carbon and total sulfur abundance when compared to the rest of the section (Fig. 1).

Our closer examination of the upper mound-bearing unit (Fig. 2) revealed the presence of sponge fossils in close association with stromatolites within the mounds (Figs. 3 and 4). The abundance of sponges varies within each mound, but we estimate that sponges make up 20%–30% of any given mound (Fig. 4; Fig. DR1 in the GSA Data Repository¹). The sponges are observed growing on top of stromatolites, between stromatolites, and are encrusted by stromatolites (Fig. 4). The shape of the stromatolites is often a function of the shape of the encrusted sponge (Figs. 3C and 3D). Although spicules currently consist of calcite

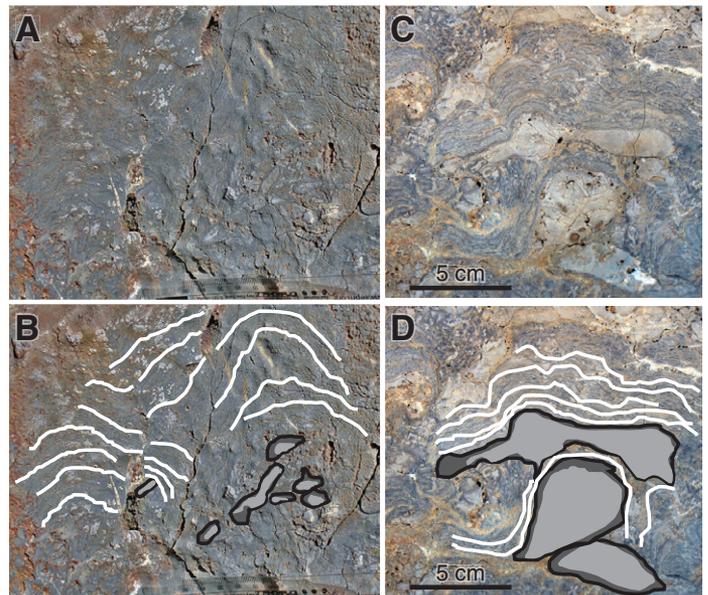


Figure 3. A: Closeup of outcrop photograph showing spatial relationships between stromatolites and sponges. B: Same view as A, but with some of stromatolitic laminations and sponge fossils traced. Ruler near bottom of each photograph is ticked for 5 cm. C: Outcrop photograph of different mound showing spatial relationships between stromatolites and sponges. D: Same view as in C, but with some stromatolitic laminations and sponges traced. Note that stromatolites take their shape from that of encrusted sponge.

microspar, perpendicular intersection of rays suggests that these were originally hexactinellid spicules made of silica (Fig. DR2).

Fragmentary bivalves, gastropods, ostracods, and echinoderm plates occur within, above, and between mounds of both units. Articulated bivalved shells are preserved within the central cavities of sponges in the upper unit mounds (Fig. 5; Fig. DR3). The microbialites of both mound-bearing units consist of a combination of stromatolites and thrombolites. Discrete trace fossils occur within the stromatolitic laminations of the upper mound-bearing unit (Fig. 5). Because the laminations surrounding the disruption are not only truncated but also pulled down, these structures are best classified as burrows formed while the substrate was not yet fully lithified, as opposed to borings in hard substrate.

¹GSA Data Repository item 2012198, supplemental figures, is available online at www.geosociety.org/pubs/ft2012.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

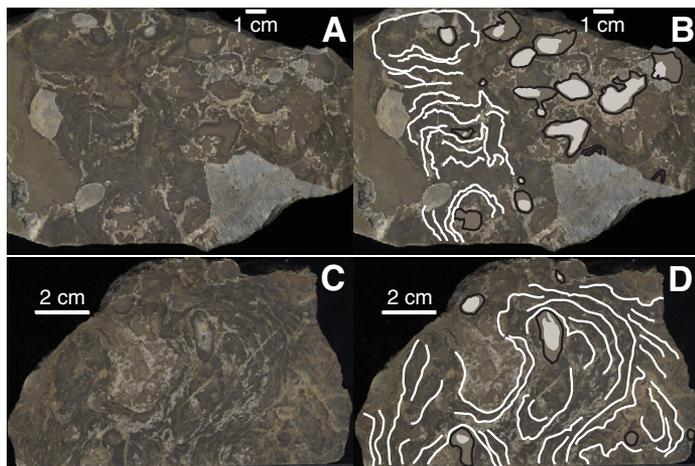


Figure 4. A: Photograph of polished slab showing vertical cut through stromatolite and multiple sponge fossils. B: Same view as A, but with some of stromatolitic laminations and sponge fossils traced. C: Photograph of polished slab showing horizontal cut (i.e., bedding-parallel cut) through multiple stromatolites and sponges. D: Same view as C, but with some of stromatolitic laminations and sponge fossils traced. Note that sponges and stromatolites encrust each other.

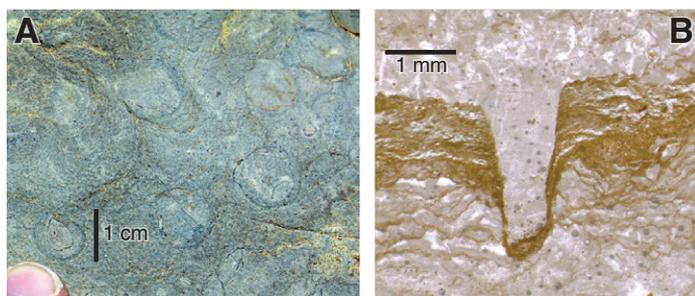


Figure 5. A: Bedding-plane view of top of upper unit mound in outcrop showing several sponges. Sponge to left and adjacent to scale bar contains articulated bivalved shell in its cavity. B: Photomicrograph of burrow in stromatolitic lamination from upper mound-bearing unit.

DISCUSSION

Previous workers who have studied the microbialite mounds of the Virgin Limestone interpreted them to indicate deleterious conditions following the end-Permian mass extinction (Pruss and Bottjer, 2004; Woods, 2009; Mata and Bottjer, 2011). Although our data do not rule out short-lived deleterious or unusual conditions, the low abundances of organic carbon and total sulfur suggest that anoxia was not prevalent during the deposition of the Virgin Limestone at Lost Cabin Spring. Organic carbon abundances tend to be high in anoxic environments due to the limitation of aerobic decomposers (e.g., Arthur and Sageman, 1994). Similarly, bacterial sulfate reduction in anoxic environments tends to lead to high abundances of sulfide, a byproduct of sulfate reduction (e.g., Berner, 1970). An alternative explanation for the low organic carbon abundances is decreased production of organic matter in the water column. However, this interpretation is not favored given the total sulfur data and the observed mound ecology (see following). Evidence for anoxia in the more distal, deeper water environments of the Union Wash Formation suggests that anoxia was likely present in the deep ocean (Woods et al., 1999; Woods and Bottjer, 2000; but see Heydari et al., 2003). If such anoxic water were to transgress onto the shelf, as has been suggested (Pruss and Bottjer, 2004; Woods, 2009; Mata and Bottjer, 2011), the anoxia did not persist long enough to allow for the accumulation of significant amounts of organic carbon and pyrite.

Our investigation revealed that the two mound-bearing units at Lost Cabin Spring are quite different. Whereas the larger mounds of the lower unit may have been favored by the suppression of metazoan grazers (Schubert and Bottjer, 1992; Pruss and Bottjer, 2004), the mounds of the upper unit are much more ecologically complex. The participation of metazoans in reef framework building is an ecological step above the buildups that have been reported to date (Pruss et al., 2007; Brayard et al., 2011). Here we demonstrate that both sponges and stromatolites contributed to the patch reef frameworks by mutual encrustation to form large mounds with relief above the seafloor. The multiple occurrences of bivalved fossils preserved within sponge bodies suggest that individual sponges may have acted as habitat for benthic invertebrates. These animals may have been benefiting from the excurrent flow of water from the sponges, as has been reported from the modern record (Pansini et al., 1999).

In addition to the low organic carbon and total sulfur abundances, the occurrence of discrete burrows within the stromatolites of the upper mound unit argues against anoxia during the formation of the younger mounds. The fact that the burrows likely formed while the substrate was still soft suggests that there must have been sufficient oxygen in the water column to support grazers during the formation of the stromatolites of the upper mound-bearing unit. Because we have yet to find such burrows in the stromatolites of the lower mound-bearing unit, we cannot rule out periodic anoxia contributing to their formation. However, the geochemical data presented here argue against sustained anoxia during the deposition of the entire section. Our results may suggest differences between shallow-marine environments of the Tethys and Panthalassa (e.g., Kershaw et al., 2009).

The lower unit stromatolite mounds are still unusual for Phanerozoic patch reefs in that metazoans did not contribute to framework building (Pruss and Bottjer, 2004). However, we interpret the stromatolite-sponge mounds of the upper unit to represent the transition to biotic recovery at this locality because of their ecologic complexity, as has been interpreted for other localities (Brayard et al., 2011). These results contribute to our evolving understanding of the aftermath of and biotic recovery from the end-Permian mass extinction.

ACKNOWLEDGMENTS

We thank Caity Tully, Sascha Patel, Erin Miller, and Scott Schaefer for invaluable field assistance. We also thank Bryn Mawr College and Haverford College students Rachel Lubitz, Erin Lynch, David Wicks, Sheba Brown, and Caity Tully for help with geochemical analysis. This work was funded by National Science Foundation award 0921127. This work benefited from insightful comments from two anonymous reviewers.

REFERENCES CITED

- Arthur, M.A., and Sageman, B.B., 1994, Marine black shales; depositional mechanisms and environments of ancient deposits: *Annual Review of Earth and Planetary Sciences*, v. 22, p. 499–551, doi:10.1146/annurev.earth.22.050194.002435.
- Baud, A., Richoz, S., and Marcoux, J., 2005, Calcimicrobial cap rocks from the basal Triassic units: Western Taurus occurrences (SW Turkey): *Comptes Rendus Palévol*, v. 4, p. 569–582, doi:10.1016/j.crpv.2005.03.001.
- Baud, A., Richoz, S., and Pruss, S., 2007, The lower Triassic anachronistic carbonate facies in space and time: *Global and Planetary Change*, v. 55, p. 81–89, doi:10.1016/j.gloplacha.2006.06.008.
- Baud, A., Nakrem, H.A., Beauchamp, B., Beatty, T.W., Embry, A.F., and Henderson, C.M., 2008, Lower Triassic bryozoan beds from Ellesmere Island, High Arctic, Canada: *Polar Research*, v. 27, p. 428–440, doi:10.1111/j.1751-8369.2008.00071.x.
- Berner, R.A., 1970, Sedimentary pyrite formation: *American Journal of Science*, v. 268, p. 1–23, doi:10.2475/ajs.268.1.1.
- Blakey, R.C., 1974, Stratigraphic and depositional analysis of the Moenkopi Formation, southeastern Utah: *Utah Geological and Mineral Survey Bulletin*, v. 104, p. 1–81.
- Brayard, A., Escarguel, G., Bucher, H., Monnet, C., Brühwiler, T., Goudemand, N., Galfetti, T., and Guex, J., 2009, Good genes and good luck: Ammonoid diversity and the end-Permian mass extinction: *Science*, v. 325, p. 1118–1121, doi:10.1126/science.1174638.
- Brayard, A., Vennin, E., Olivier, N., Bylund, K.G., Jenks, J., Stephen, D.A., Bucher, H., Hofmann, R., Goudemand, N., and Escarguel, G., 2011, Transient

- metazoan reefs in the aftermath of the end-Permian mass extinction: *Nature Geoscience*, v. 4, p. 693–697, doi:10.1038/ngeo1264.
- Corsetti, F.A., Baud, A., Marengo, P.J., and Richoz, S., 2005, Summary of Early Triassic carbon isotope records: *Comptes Rendus Palévol*, v. 4, p. 473–486, doi:10.1016/j.crpv.2005.06.004.
- Erwin, D.H., 1993, *The great Paleozoic crisis: Life and death in the Permian*: New York, Columbia University Press, 327 p.
- Fraiser, M.L., and Bottjer, D.J., 2007, Elevated atmospheric CO₂ and the delayed biotic recovery from the end-Permian mass extinction: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 252, p. 164–175, doi:10.1016/j.palaeo.2006.11.041.
- Grice, K., Changqun, C., Love, G.D., Boettcher, M.E., Twitchett, R.J., Grosjean, E., Summons, R.E., Turgeon, S.C., Dunning, W., and Jin, Y., 2005, Photic zone euxinia during the Permian-Triassic superanoxic event: *Science*, v. 307, p. 706–709, doi:10.1126/science.1104323.
- 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, doi:10.1016/S0031-0182(03)00258-X.
- Holser, W.T., 1984, Gradual and abrupt shifts in ocean chemistry during Phanerozoic time, in Holland, H.D., and Trendall, A.F., eds., *Patterns of change in Earth evolution*: New York, Springer-Verlag, p. 123–143.
- Kamo, S.L., Czamanske, G.K.A.Y., Fedorenko, V.A.D.D.W., and Trofimov, V.R., 2003, Rapid eruption of Siberian flood-volcanic rocks and evidence for coincidence with the Permian-Triassic boundary and mass extinction at 251 Ma: *Earth and Planetary Science Letters*, v. 214, p. 75–91, doi:10.1016/S0012-821X(03)00347-9.
- Kershaw, S., Zhang, T., and Lan, G., 1999, A ?microbialite carbonate crust at the Permian-Triassic boundary in south China, and its palaeoenvironmental significance: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 146, p. 1–18, doi:10.1016/S0031-0182(98)00139-4.
- Kershaw, S., Crasquin, S., Collin, P.-Y., Li, Y., Feng, Q., and Forel, M.-B., 2009, Microbialites as disaster forms in anachronistic facies following the end-Permian mass extinction: A discussion: *Australian Journal of Earth Sciences*, v. 56, p. 809–813, doi:10.1080/08120090903002623.
- Knoll, A.H., Bambach, R.K., Payne, J.L., Pruss, S., and Fischer, W.W., 2007, Paleophysiology and end-Permian mass extinction: *Earth and Planetary Science Letters*, v. 256, p. 295–313, doi:10.1016/j.epsl.2007.02.018.
- Korte, C., Kozur, H.W., Bruckschen, P., and Veizer, J., 2003, Strontium isotope evolution of Late Permian and Triassic seawater: *Geochimica et Cosmochimica Acta*, v. 67, p. 47–62, doi:10.1016/S0016-7037(02)01035-9.
- Krystyn, L., Richoz, S., Baud, A., and Twitchett, R.J., 2003, A unique Permian-Triassic boundary section from the Neotethyan Hawasina Basin, central Oman Mountains: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 191, p. 329–344, doi:10.1016/S0031-0182(02)00670-3.
- Kump, L.R., Pavlov, A.A., and Arthur, M.A., 2005, Massive release of hydrogen sulfide to the surface ocean and atmosphere during intervals of oceanic anoxia: *Geology*, v. 33, p. 397–400, doi:10.1130/G21295.1.
- Lehrmann, D.J., Ramezani, J., Bowring, S.A., Martin, M.W., Montgomery, P., Enos, P., Payne, J.L., Orchard, M.J., Wang, H., and Wei, J., 2006, Timing of recovery from the end-Permian extinction: geochronologic and biostratigraphic constraints from south China: *Geology*, v. 34, p. 1053–1056, doi:10.1130/G22827A.1.
- Marengo, P.J., Corsetti, F.A., Kaufman, A.J., and Bottjer, D.J., 2008, Environmental and diagenetic variations in carbonate associated sulfate: An investigation of CAS in the Lower Triassic of the western U.S.A: *Geochimica et Cosmochimica Acta*, v. 72, p. 1570–1582, doi:10.1016/j.gca.2007.10.033.
- Mata, S.A., and Bottjer, D.J., 2011, Origin of Lower Triassic microbialites in mixed carbonate-siliciclastic successions; ichnology, applied stratigraphy, and the end-Permian mass extinction: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 300, p. 158–178, doi:10.1016/j.palaeo.2010.12.022.
- McKee, E.D., 1954, Stratigraphy and history of the Moenkopi Formation of Triassic age: *Geological Society of America Memoir* 61, 133 p.
- 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, doi:10.1126/science.1101012.
- Nielsen, J., and Shen, Y., 2004, Evidence for sulfidic deep water during the Late Permian in the East Greenland Basin: *Geology*, v. 32, p. 1037–1040, doi:10.1130/G20987.1.
- Orchard, M.J., 2007, Conodont diversity and evolution through the latest Permian and Early Triassic upheavals: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 252, p. 93–117, doi:10.1016/j.palaeo.2006.11.037.
- Pansini, M., Cattanea Vietti, R., and Shiaporelli, S., 1999, Relationship between sponges and a taxon of obligatory inquilines: The siliquariid molluscs: *Memoirs of the Queensland Museum*, v. 44, p. 427–437.
- Payne, J.L., and Clapham, M.E., 2012, End-Permian mass extinction in the oceans: An ancient analog for the twenty-first century?: *Annual Review of Earth and Planetary Sciences*, v. 40, doi:10.1146/annurev-earth-042711-105329.
- Payne, J.L., Lehrmann, D.J., Wei, J., 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, doi:10.1126/science.1097023.
- Poborski, S.J., 1954, Virgin Formation (Triassic) of the St. George, Utah, area: *Geological Society of America Bulletin*, v. 65, p. 971–1006, doi:10.1130/0016-7606(1954)65[971:VFTOTS]2.0.CO;2.
- Pruss, S.B., and Bottjer, 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, doi:10.1016/j.palaeo.2004.05.002.
- Pruss, S.B., and Payne, J.L., 2009, Early Triassic microbial spheroids in the Virgin Limestone Member of the Moenkopi Formation, Nevada, USA: *Palaios*, v. 24, p. 131–136, doi:10.2110/palo.2007.p07-094r.
- Pruss, S.B., Bottjer, D.J., Corsetti, F.A., and Baud, A., 2006, A global marine sedimentary response to the end-Permian mass extinction: Examples from southern Turkey and the western United States: *Earth-Science Reviews*, v. 78, p. 193–206, doi:10.1016/j.earscirev.2006.05.002.
- Pruss, S.B., Payne, J.L., and Bottjer, D.J., 2007, Placunopsis bioherms: The first metazoan buildups following the end-Permian mass extinction: *Palaios*, v. 22, p. 17–23, doi:10.2110/palo.2005.p05-050r.
- Riccardi, A.L., Arthur, M.A., and Kump, L.R., 2006, Sulfur isotopic evidence for chemocline upward excursions during the end-Permian mass extinction: *Geochimica et Cosmochimica Acta*, v. 70, p. 5740–5752, doi:10.1016/j.gca.2006.08.005.
- Schubert, J.K., and Bottjer, D.J., 1992, Early Triassic stromatolites as post-mass extinction disaster forms: *Geology*, v. 20, p. 883–886, doi:10.1130/0091-7613(1992)020<0883:ETSAPM>2.3.CO;2.
- Twitchett, R.J., Krystyn, L., Baud, A., Wheelley, J.R., and Richoz, S., 2004, Rapid marine recovery after the end-Permian mass-extinction event in the absence of marine anoxia: *Geology*, v. 32, p. 805–808, doi:10.1130/G20585.1.
- Woods, A.D., 2009, Anatomy of an anachronistic carbonate platform: Lower Triassic carbonates of the southwestern United States: *Australian Journal of Earth Sciences*, v. 56, p. 825–839, doi:10.1080/08120090903002649.
- Woods, A.D., and Bottjer, D.J., 2000, Distribution of ammonoids in the Lower Triassic Union Wash Formation (eastern California); evidence for paleoceanographic conditions during recovery from the end-Permian mass extinction: *Palaios*, v. 15, p. 535–545, doi:10.1669/0883-1351(2000)015<0535:DOAITL>2.0.CO;2.
- 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, doi:10.1130/0091-7613(1999)027<0645:LTLTLC>2.3.CO;2.

Manuscript received 19 October 2011

Revised manuscript received 16 February 2012

Manuscript accepted 1 March 2012

Printed in USA