Investigating the Paleoecological Consequences of Supercontinent Breakup: Sponges Clean Up in the Early Jurassic

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ABSTRACT

The continued release of fossil fuel carbon into the atmosphere today means it is imperative to understand Earth system response to CO_2 rise, and the geologic record offers unique opportunities to investigate such behavior. Stomatal and paleosol proxies demonstrate a large change in atmospheric pCO_2 across the Triassic-Jurassic (T-J) transition, concomitant with the eruption and emplacement of the Central Atlantic Magmatic Province (CAMP) and the splitting of Pangea. As one of the "big 5" mass extinctions—when the so-called modern fauna was particularly hard hit—we know the biosphere was severely affected during this time, but the details are relatively poorly understood, particularly with respect to an Earth system perspective. As part of the NSF Earth Life Transitions initiative, our team has targeted the T-J for integrative investigation to explore, among other things, alternative ecological states that may exist in the aftermath of mass extinctions. The initial findings reveal a global "sponge takeover" in the Early Jurassic following the extinction that lasted nearly 2 million years. The sponge takeover may be linked to an unusual confluence of factors, including potential ocean acidification and intense silicate weathering following the emplacement of CAMP.

INTRODUCTION

The Triassic-Jurassic (T-J) interval represents a slice of deep time when the Earth experienced a rapid rise in pCO_2 (e.g., McElwain et al., 1999; Beerling and Berner, 2002; Berner and Beerling, 2007; Steinthorsdottir et al., 2012; Schaller et al., 2011, 2012) resulting from the initial splitting of the supercontinent Pangea and the emplacement of the Central Atlantic Magmatic Province (CAMP), one of the largest igneous provinces in Earth's history (e.g., Marzoli et al., 1999; McHone, 2002; Nomade et al., 2007) (Figure 1). Estimates of eruption rates vary, but CO_2 input could have been on the order of ~13.2 Gt/CO_2 per year, rivaling modern input rates (~36 Gt/CO_2 per year) (e.g., Schaller et al., 2011, 2012). The iconic Palisades Sill overlooking the Hudson River is a classic example of CAMP magmatism (e.g., Blackburn et al., 2013). Via some estimates (e.g., Marzoli et al., 1999; Olsen, 1999; McHone, 2002), CAMP lavas would have covered the conterminous United States with ~400 m of basalt (in other words, it was big). The rapid addition of CO_2 to the atmosphere-ocean system makes the T-J interval a candidate for ocean acidification in deep time (Hautmann et al., 2008; Greene et al., 2012; Martindale et al., 2012). And, like many mass extinctions, the organic carbon cycle appears perturbed across the boundary, with a negative carbon isotope excursion recorded in many sections (e.g., Ward et al., 2001; Guex et al., 2004; Hesselbo et al., 2004; Williford et al., 2007)

The T-J interval includes one of the "big 5" mass extinctions, a critical transition for life on Earth (e.g., Raup and Sepkoski, 1982) (Figure 1). Notably, representatives of the fauna that inhabit today's seas (the so-called modern fauna *sensu* Sepkoski, 1981), and animals living in reef and carbonate-dominated environments were preferentially negatively affected by the end Triassic mass extinction (Alroy, 2010; Kiessling and Simpson, 2011; Kiessling et al., 2007). Furthermore, it was the first major extinction experienced by scleractinian corals (Kiessling and Simpson, 2011; Kiessling et al., 2007) (Figure 1). Thus, the end-Triassic mass extinction is
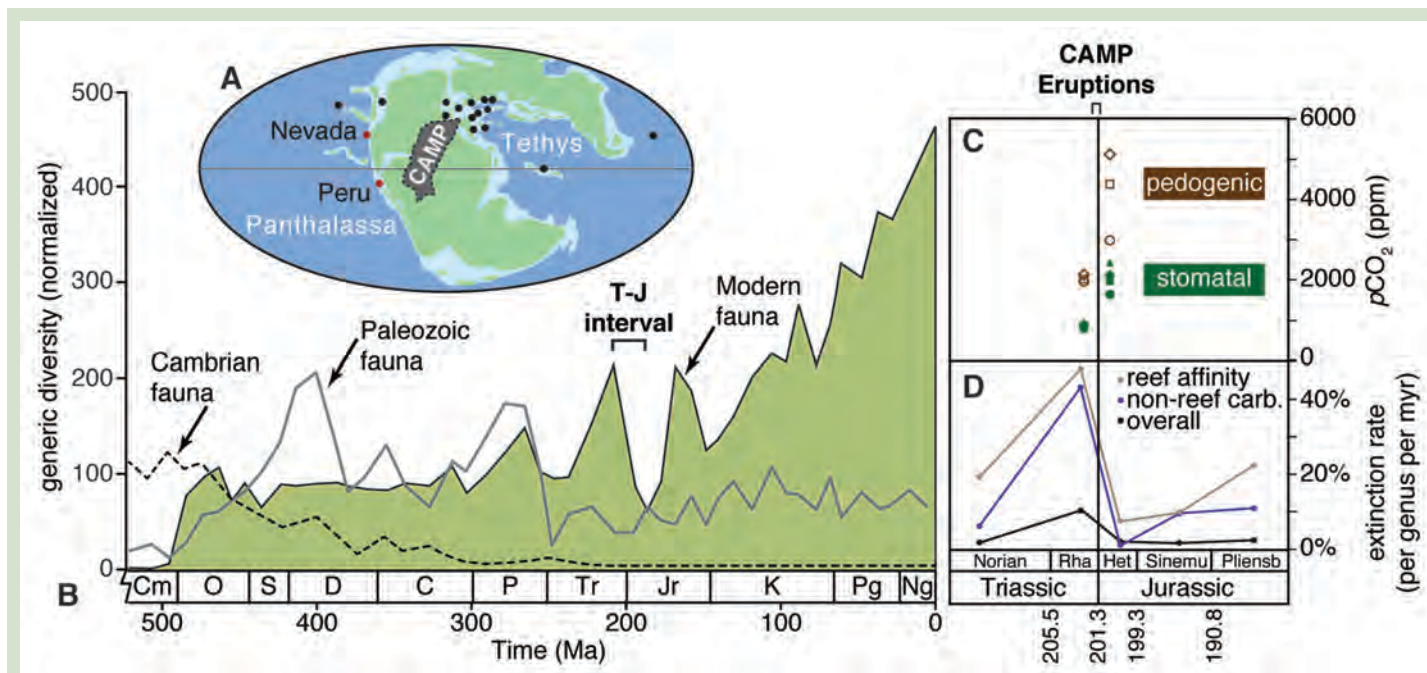
Figure 1: Summary of features associated with the T-J interval. A) Paleogeographic map of the T-J, with key localities and the hypothesized extent of CAMP marked (modified from Greene et al., 2012). B) Generic diversity of the Cambrian, Paleozoic, and Modern Faunas, highlighting that the T-J extinction was particularly devastating to the Modern Fauna (Alroy 2010). C) Summary of pCO² levels across the T-J from stomatal proxies (green) and pedogenic proxies (brown) (symbols for stomatal and pedogenic proxies represent individual localities as discussed in Martindale et al., 2012). D) Extinction rate across the T-J interval, highlighting preferential extinction of fauna associated with carbonate environments and reefs (Kiessling and Simpson, 2011; Kiessling et al., 2007).

especially relevant for understanding the present-day impact of rising CO_2 levels on the marine biosphere (Figure 1). The T-J interval, as used here, refers to the lead up to the extinction in the latest Norian and Rhaetian stages (the last two stages of the Triassic, respectively) through the Hettangian and early Sinemurian Stages (the first two stages of the Jurassic, respectively), where the extinction event horizon itself is in the latest Triassic (Rhaetian Stage).

Typically, the biotic response to mass extinction events is treated as a "numbers game", where the loss of standing diversity is the focus, followed by some "recovery" in the number of taxa in the aftermath of the extinction. But what defines recovery? Simply focusing on a return to pre-extinction levels of diversity deemphasizes potentially interesting and important alternate ecological states (e.g., Hull and Darroch 2013). As such, unraveling the marine paleoecology in the aftermath of the extinction has been a major focus of our recent studies. Here, we present

some preliminary results from two of our major field areas—Nevada and Peru—to highlight the concept of an unexpected "alternate ecological state" in the aftermath of extinction.

UNEXPECTED POST-EXTINCTION ECOLOGY: SPONGES CLEAN UP IN THE EARLY JURASSIC OF NEVADA

In west central Nevada, the Gabbs and Sunrise Formations of the Gabbs Valley Range comprise an excellent, well-exposed Triassic – Jurassic shallow shelf depositional sequence (Figures 2 and 3). It was once in the running to become the global stratotype section and point (GSSP) (e.g., Lucas et al., 2007). The strata were deposited in a basin between the Sierran arc and the North American continent in eastern Panthalassa (Figure 1) (e.g., Stewart, 1980). Comprehensive mapping (e.g., Muller and Ferguson 1939), biostratigraphy (e.g., Guex et al., 2004), chemostratigraphy (Guex et al., 2004;

Ward et al., 2007) and paleontological research (e.g., Laws 1982; Taylor et al., 1983) set the stage for our studies.

The uppermost Triassic strata of the Mount Hyatt Member of the Gabbs Formation represent a typical, prolific Late Triassic carbonate ramp assemblage, including massive fossiliferous wackestones and thin-bedded mudstones (e.g., Laws 1982). The shift to siliciclastic-dominated sedimentation in the overlying Muller Canyon Member of the Gabbs Formation represents a collapse of the vibrant carbonate system in association with the mass extinction (e.g., Lucas et al., 2007). The shales, siltstones, and fine sandstones of the Muller Canyon Member contain the Triassic/Jurassic boundary. The lower to middle Muller Canyon Member has been previously interpreted to represent a regression (Laws, 1982), a transgression (Hallam and Wignall, 2000), or a transgression-regression couplet (Schoene et al., 2010). Recent macro-, meso-, and microscale facies analysis demonstrate

very little/subtle sedimentary change throughout the lower two thirds of the Muller Canyon Member. Laminated siltstones and rare very fine sandstones with low amplitude hummocky cross stratification indicate a position below fair-weather wave base/near storm wave base on the middle to inner shelf, similar to the underlying carbonate-dominated Mount Hyatt Member. Rather than recording a significant depth change, it appears that metazoan-dominated carbonates are simply not present in the Muller Canyon Member. Beds gradually increase in thickness in the upper Muller Canyon Member, until their transition to thin-bedded silty carbonates of the overlying carbonate-rich Sunrise Formation and

the eventual return of carbonate ramp deposition (e.g., Lucas et al., 2007; Ritterbush et al., 2014).

After the last occurrence of the uppermost Triassic ammonite *C. crickmayi* in the Muller Canyon Member, shelly benthic fossil content drops dramatically, to essentially undetectable levels, marking the extinction event (Figures 2 and 3). This interval is also characterized by the initial negative carbon isotope excursion seen worldwide (Figures 2 and 3), and the subsequent 7 meters are considered the Extinction Interval (Figure 3). The base of the Jurassic is defined by the first appearance of the ammonite *P. spelae* (Guex et al., 2004), but the ecosystem had by no

means recovered to a pre-extinction state. Rather, macroscopic benthic fossils remain rare and are not detected in thin section in most of the Jurassic Muller Canyon Member strata (~10 m, which we term the Depauperate Zone in Figures 2 and 3) (Ritterbush et al., 2014). While a slightly greater abundance of ammonoids is noted in the Depauperate Zone, benthic fossils are limited to isolated occurrences of rare *Modiolus* mussel clusters, small *Agerclamys* scallops, preserved primarily as casts without substantial shell material (see also Taylor et al., 1983; Hallam and Wignall, 2000; Ward et al., 2007; Taylor et al., 2007), and rare 4-6 cm-deep *Helminthoides* or individual *Rhizocorallium* burrows.
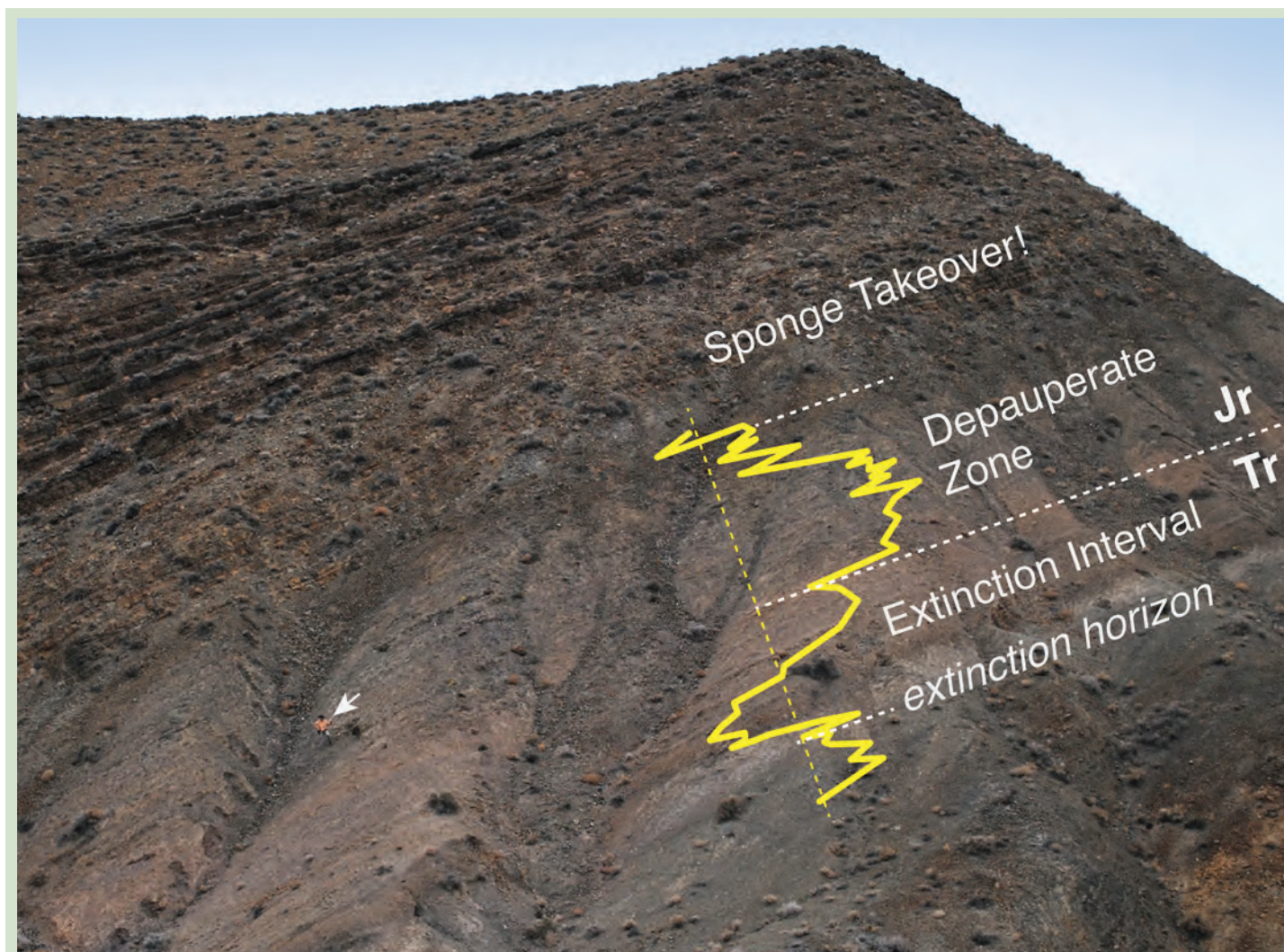

Figure 2: Photograph of Ferguson Hill, Muller Canyon, Nevada. Carbon isotope profile from Ward et al. (2007) (isotopic scale is given in Fig. 3), corrected for the presence of a fault. Note paleobiologist, for scale.
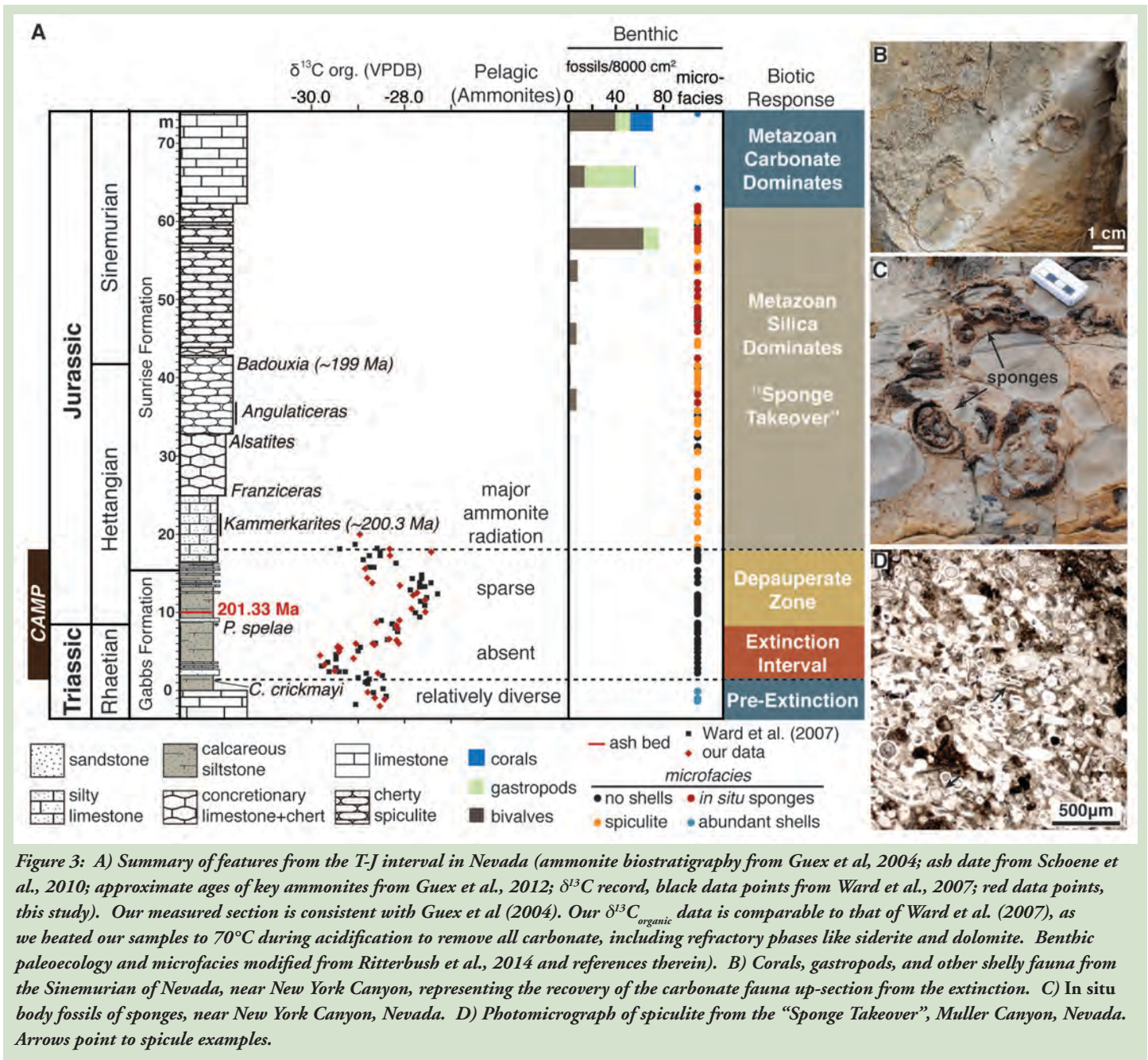
Figure 3: A) Summary of features from the T-J interval in Nevada (ammonite biostratigraphy from Guex et al, 2004; ash date from Schoene et al., 2010; approximate ages of key ammonites from Guex et al., 2012; $\delta^{13}C$ record, black data points from Ward et al., 2007; red data points, this study). Our measured section is consistent with Guex et al (2004). Our $\delta^{13}C_{organic}$ data is comparable to that of Ward et al. (2007), as we heated our samples to 70°C during acidification to remove all carbonate, including refractory phases like siderite and dolomite. Benthic paleoecology and microfacies modified from Ritterbush et al., 2014 and references therein). B) Corals, gastropods, and other shelly fauna from the Sinemurian of Nevada, near New York Canyon, representing the recovery of the carbonate fauna up-section from the extinction. C) In situ body fossils of sponges, near New York Canyon, Nevada. D) Photomicrograph of spiculite from the "Sponge Takeover", Muller Canyon, Nevada. Arrows point to spicule examples.

The main lower Jurassic ammonite diversification occurs near the base of the Ferguson Hill Member of the Sunrise Formation, indicating a major radiation of pelagic forms (e.g., Guex et al., 2004), and a more robust recovery in the pelagic realm. Interestingly, via correlation with radiometrically-dated successions (e.g., Peru; Guex et al., 2012), the radiation is nearly coincident with the cessation of CAMP volcanism (Blackburn et al., 2013); that is, the start of a more robust recovery did not occur until CAMP volcanism terminated. Shelly faunas, however,

remain extremely depauperate, both in abundance and diversity, and the return of carbonate bedding is not accompanied by a dramatic increase in macroscopic shell content as might be expected, a finding paralleled at the microscopic level (Ritterbush et al., 2014).

Unexpectedly, the next 40 meters of strata, representing the remaining Hettangian Stage and the lower part of the Sinemurian Stage, are replete with sponge spicules (Ritterbush et al., 2014), first via 20 m of abundant transported siliceous sponge spicules,

next via spicule-filled burrows, and finally via pure spiculite including *in situ* siliceous sponges (Ritterbush et al., 2014) (Figure 3 C, D). For the first time since the extinction horizon, metazoans become a major constituent in the sedimentary record, potentially indicating a significant recovery in the benthic realm. But rather than carbonate producers, it is siliceous demosponges that take over the shelf, reflecting an interesting alternative-ecosystem-state in the aftermath of extinction. Styles (simple spicules), dichotriaenes (complex

Figure 4: A) Field image of the T-J interval, Pucará Basin, Peru (Malpaso Section, Ritterbush et al., 2015). B) Photomicrograph of spiculite from the Aramachay Formation, Morococha section, Peru; arrows point to spicule examples.

spicules), and desmid spicules (highly mineralized spicules) of astrophorid demosponges dominate the spiculites. Abundant carbonate storm beds in the cherty interval support a middle shelf depositional environment and blanket *in situ* sponges in some cases. These sedimentological observations indicate that carbonate sedimentation was present, but sponges—silica, not carbonate—constituted the major metazoan contribution to sediments. The remaining strata record an abrupt shift to carbonate-dominated bioclastic wackestones, packstones, and ooid-rich grainstones, heralding the return of a robust carbonate ramp, including a return of corals, bivalves, and gastropods (Figure 3B), marking the next step in the recovery of the ecosystem from the end-Triassic extinction.

A GLOBAL SPONGE TAKEOVER?

Sponge hegemony characterizes the early Jurassic of Nevada, but is the takeover a local phenomenon or does it have global significance? Previous publications hinted that sponge deposits existed in the Pucará Group, Peru (Szekely and Grose, 1972; Rosas et al., 2007). Our recent work with collaborator Silvia Rosas demonstrates that, like Nevada, shallow water facies of the T-J Aramachay Formation, Pucará Group, Peru, record abundant spiculites, spiculite filled burrows, and *in situ* sponge body fossils (Ritterbush et al., 2015). In fact, some strata of the

Aramachay Formation (Figure 4) appear nearly identical to their counterparts in Nevada. The Hettangian sponge phenomenon extends throughout Europe (Austria, France), as well as Morocco (e.g., Delecat et al., 2010; Neuweiler et al., 2001). Many of the European localities represent deeper paleoenvironments, so the siliceous sponge accumulations may not have been considered unusual, given the modern distribution of siliceous sponges in the deep whereas they are more remarkable in the stratigraphically expanded shallow water occurrences in Nevada and Peru.

WHY SPONGES?

During recoveries from global mass extinctions, ecological complexity is expected to expand through a succession of trophic levels (e.g., Sole et al., 2002), but novel scenarios may emerge via chance ecological or environmental opportunities (e.g., Hull and Darroch, 2013). We hypothesize that the T-J "sponge takeover" resulted from the unique confluence of ecological and environmental circumstances in the aftermath of the end-Triassic mass extinction. Ecologically, the decimation of previously dominant calcifiers during the Triassic-Jurassic transition likely eliminated incumbency challenges to sponges settling across the shelf. In modern reef settings, it is not uncommon for sponges to initially colonize areas vacated by corals, only to have the corals retake the real estate

on ecological time scales. The full two million year occupation, however, is a geologic-scale event, and most models of ocean acidification, which would suppress the carbonate producers, last perhaps tens of thousands of years, not millions (e.g., Hönisch et al., 2012); mere ecological patterns do not offer a satisfying explanation without input from the broader environment.

Silica constitutes a major nutrient for silica sponges, and may hold some of the answers for the duration and timing of the T-J sponge event. The rifting of Pangea and eruption of CAMP is likely to have affected silica supply by increasing weathering fluxes, the primary silica source to the oceans. Increases in atmospheric pCO_2 would have intensified silicate weathering delivering additional silica to the oceans (e.g., Berner and Beerling, 2007; Schaller et al., 2011). Presence of the CAMP basalts should have further increased weathering fluxes of silica; weathering is faster on fresh rock, and is observed to be five times faster on basalts compared to granites (West et al., 2011).

The types of spicules produced by sponges, and the rates of silica uptake, depend on silica concentration (Maldonado et al., 1999; Reincke and Berthel, 1997) and may provide further evidence for enhanced silica supply during the sponge takeover. Desma spicules, which are more robust and can interlock, are ubiquitous in the Nevada and Peru Early Jurassic deposits (Ritterbush et al., 2015;

2015). Desmas are produced by a broad variety of sponges if silica concentration is sufficient (e.g., 30-100 µm; Maldonado et al., 1999), and thus may constitute evidence for elevated silica concentrations during the sponge takeover. A box model investigating the T-J silica budget provided in Ritterbush et al. (2015) is also consistent with the aforementioned scenario. Thus, the sponge event likely originated from a cascade of events following the rifting of Pangea and eruption of CAMP: CAMP CO_2 initially caused ocean acidification, suppressing the incumbent coral reefs, then, on a longer time scale, silicate weathering provided the limiting nutrient, silica, that allowed the sponges to take hold for upwards of 2 million years. The coincidence of the ecological and geochemical circumstances demonstrates why such an event is best investigated from an Earth-Life Transitions perspective.

FROM THE T-J LOOKING FORWARD

Our preliminary results from the T-J suggest that, with increased pCO_2 in the atmosphere, the potential for ocean acidification exists, silicate weathering should increase, and the flux of silica and alkalinity to the oceans should increase. Will we be faced with another sponge takeover in our future? Ocean acidification is measureable today as CO_2 builds in the atmosphere and equilibrates with the ocean—the lesson from the T-J regarding the possible effects on coral reefs (that is, they could crash) should be heeded. However, we suspect the Earth today is not headed for another sponge event, for several obvious reasons. The silica cycle is different today, predominantly controlled by diatom abundance and distribution, versus the T-J interval, which preceded the origination of diatoms. Also, CAMP would have provided an abundance of fresh basalt ripe for weathering, a situation not present in today's Earth system. Nonetheless, though we do not expect a sponge takeover, the T-J example might indicate the ramifications of providing an abundant supply of a limiting nutrient to diatoms as a result of increased weathering in a warmer climate must be considered as a potential marine consequence of anthropogenic CO_2 release, in addition to the deleterious effects of increased pCO_2 on coral reefs. More generally, the T-J sponge takeover represents an excellent example of "alternative ecological states" perhaps not predicted via the typical actualistic view of the Earth system, and a manifestation of the law of unintended consequences.

ACKNOWLEDGEMENTS

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