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Experimental evidence supports early silica cementation of the Ediacara Biota

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ABSTRACT

Casts and molds of soft-bodied organisms in Ediacaran sandstones ("Ediacara-style" fossilization) have played an important role in reconstruction of the emergence and radiation of early complex macroscopic life. However, the preservational processes responsible for the Ediacara fossil record are still vigorously debated. Whereas classic studies proposed fossilization via rapid sulfide mineralization of carcass and matground surfaces, a more recent view posits silica as the key mineral involved in their preservation. We performed experiments in which a variety of soft-bodied organisms were exposed to silica-rich solutions at concentrations considered characteristic of Ediacaran seawater (2 mM). Our results document continuous precipitation of amorphous silica onto the surfaces of these organic tissues under constant and normal marine pH values (7.8). Mineral formation was accompanied by a progressive decrease in the dissolved silica (DSi) concentration of the experimental solution to levels well below amorphous silica saturation. Additionally, we find that the magnitude of silica precipitation is correlated to each organism's functional-group chemistry, as measured by potentiometric acid-base titrations. We suggest that a wide range of soft-bodied organisms were prone to silicification in Ediacaran marine environments characterized by anactualistically high DSi concentrations. This provides further support for the model that the extraordinary moldic preservation of the Ediacara Biota was promoted by early silica cementation and that this mode of preservation can offer an accurate glimpse into the composition of those early animal ecosystems.

INTRODUCTION

The exceptionally well-preserved Ediacara Biota (571–541 Ma) provides a unique window into the emergence of early complex life and the rise of animal-dominated ecosystems on Earth. These extraordinary and enigmatic fossils are best known from moldic preservation of soft tissues in sandstones ("Ediacara-style" preservation; cf. Tarhan et al., 2016). Instances of Ediacara-style preservation span the Mesoproterozoic to the Devonian but are unknown from younger successions (Tarhan et al., 2016), suggesting that this mode of fossilization may have required anactualistic (without modern analogue) conditions or processes (e.g., Gehling, 1999; Tarhan et al., 2016; MacGabhann et al., 2019; Bobrovskiy et al., 2019). Reconstruction of the identity and ecology of these ancient organisms requires a robust understanding of the mechanisms responsible for this distinctive style of preservation.

Various models have been proposed to explain the exceptional nature of Ediacara-style preservation, including molding or binding by detrital and authigenic clay minerals (Wade, 1968; Callow and Brasier, 2009; Laflamme et al., 2011; Bobrovskiy et al., 2019; Newman et al., 2019), the precipitation of iron sulfides and oxides (Gehling, 1999; Darroch et al., 2012; Liu et al., 2019; MacGabhann et al., 2019), and early silica cementation (Tarhan et al., 2016, 2019). For all models, early morphological replication of soft tissues in coarse siliciclastic sediments is integral to fossilization. However, previous paleontological, petrographic, and geochemical characterization of the Ediacara Member of South Australia—the taxonomically and ecologically richest Ediacara Biota deposit (cf. Darroch et al., 2015)—indicates that key examples of this style of fossilization are associated with pervasive early diagenetic silica cements and lack clay or early-forming iron phases (Tarhan et al., 2016, 2019). Given their ubiquity in the Ediacara Member and other Ediacara-style fossil deposits, these silica cements have been

interpreted to have played a pivotal role in this style of fossilization.

The Proterozoic and lower Paleozoic fossil record is richly populated by deposits in which fossilization has been linked to early diagenetic silica precipitation, including Bitter Springs–style preservation of organic-walled microfossils and matgrounds (Butterfield, 2003; Manning-Berg et al., 2019), silica replacement (Schubert et al., 1997), and Ediacara-style preservation (Tarhan et al., 2016). These styles of exceptional fossilization were likely mediated by high seawater dissolved silica (DSi) (H_4SiO_4) concentrations—potentially as high as 2.2 mM (the solubility of amorphous silica at 25 °C; Morey et al., 1964)—prior to the radiation of silica biomineralizers (e.g., Maliva et al., 1989; Siever, 1992). Previous studies have highlighted the importance of various organic substrates in providing reactive interfaces that promote heterogeneous nucleation and growth of amorphous silica (e.g., Leo and Barghoorn, 1976; Knoll, 1985; Siever, 1992; Konhauser et al., 2001). Therefore, high marine DSi conditions, coupled with widespread microbial matgrounds and a paucity of destructive burrowing, may have optimized globally extensive Ediacara-style fossilization during the Ediacaran (Gehling, 1999; Tarhan et al., 2016). However, the early-silica-cementation model for Ediacara-style preservation has been highly contentious (cf. Liu et al., 2019; MacGabhann et al., 2019), and one of the major objections raised has been a lack of experimental support for this model (Newman et al., 2019). Previous taphonomic experiments have mostly focused on attempts to replicate pyrite- or clay-mediated preservation of soft-bodied organisms, largely on immature sandy or clay substrates (Darroch et al., 2012; Gibson et al., 2018; Newman et al., 2019). No experiments to date have successfully replicated Ediacara-style quartzose preservation (i.e., silica precipitation in the absence of other mineral phases).
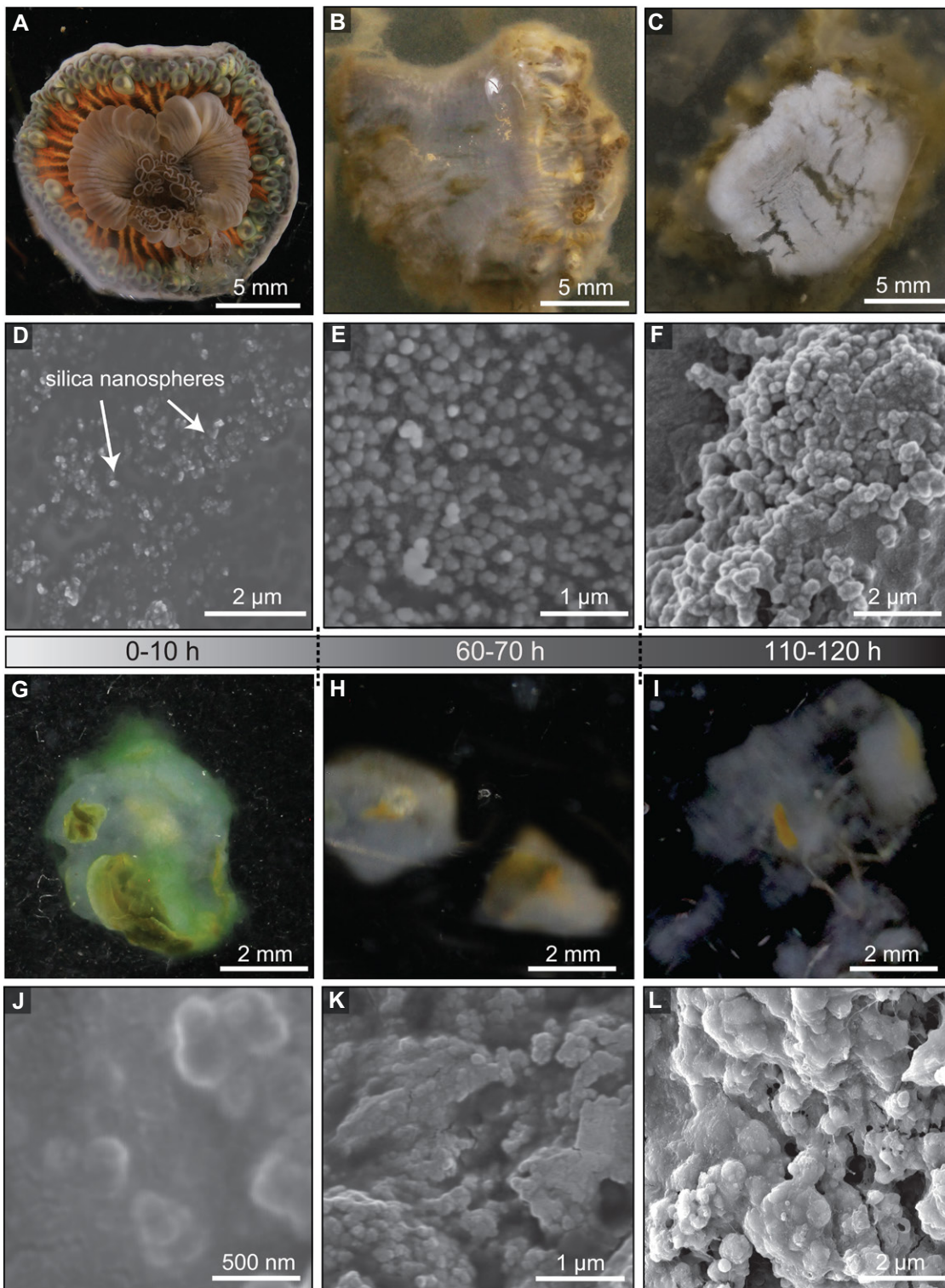
Figure 1. (A–C) Anemone *Phymanthus* exposed to high silica concentrations over time (5, 25, and 116 h, respectively). Secondary electron–scanning electron microscopy (SE-SEM) images in B and C show visible silica precipitate. (D–F) Representative SE-SEM images of *Phymanthus* show silica nanospheres increasing in size and abundance over time. (G–I) Photographs of cyanobacterium *Spirulina* aggregates exposed to high silica concentrations, with attached Si precipitates. (J–L) SE-SEM micrographs showing silica spheres associated with *Spirulina*.

To move this debate forward, we conducted taphonomic experiments testing the effects of high DSi concentrations and the surface reactivity of a variety of soft-bodied organisms in mediating amorphous silica precipitation. We show that the reactivity of the organism-seawater interface promotes silica precipitation, even on the short time scales required for preservation of soft tissues under normal marine conditions. Our experiments indicate that fossilization of macrofaunal soft tissues can occur in the absence of other mineral precipitates, providing further support for the assertion that amorphous silica cementation can occur sufficiently rapidly to have mediated the exceptional Ediacara-style fossilization of Earth's earliest animal communities.

METHODS

Specimens of the demosponge *Cinachyra alloclada*, scyphozoan medusa *Cassiopea* sp., anemone *Phymanthus crucifer,* aquatic plant *Marsilea* sp., and cyanobacterium *Spirulina* sp. were obtained from the Carolina Biological Supply Company (Burlington, North Carolina, USA); *Quercus rubra* (northern red oak) leaves were also collected (41°31′08″N, 72°92′27″W).

Each specimen was euthanized through exposure to a dark anoxic environment for 24 h, and placed in 68-mm-diameter sterile plastic jars filled with artificial seawater and maintained at room temperature while tightly capped. To assess their reactivity toward silica, potentiometric acid-base titrations coupled with surface complexation modeling were performed for each specimen across a pH range of 3.0–10.5 under 0.56 M NaCl solutions; the wide pH range facilitated measurement of the various organic ligands composing the biomass material and is not reflective of environmental conditions at the time of silicification (cf. Hao et al., 2019). The silicification experiments were initiated by adding $Na_2SiO_3 \cdot 9H_2O$ to prefiltered seawater (with 0.45 μm pore-size filters) to achieve a 2 mM Si solution, a concentration chosen to represent Ediacaran seawater (cf. Siever, 1992); 200 mL of the 2 mM Si solution was injected into each sample jar, followed by an immediate pH adjustment by the addition of 0.5 ml 1 N HCl. A pH value of 7.8 was maintained for the duration of the experiments by the addition of 1 M 3-(*N*-morpholino)propanesulfonic acid (MOPS) buffer (Table S1 in the Supplemental Material[1]). All experiments and additional abiotic control experiments were performed in triplicate. Water samples and organic tissues were extracted at sequential timed intervals to assess silica precipitation (Table S2). Detailed methods are provided in the Supplemental Material.

RESULTS

A visible silica crust (>50 μm thickness) was observed on each specimen after 110–120 h

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[1]Supplemental Material. Detailed methods, supplemental tables, and acid-base titration curves. Please visit https://doi.org/10.1130/GEOL.S.12837737 to access the supplemental material, and contact editing@geosociety.org with any questions.

of the experiment (Figs. 1B, 1C, 1G, and 1H), except for (1) the control experiments, and (2) the *Marsilea* and *Quercus* samples, which demonstrated very limited silica precipitation (Fig. S1). All organic matter in the silicified specimens decayed within the first 150 h of the experiment (Table S3). Scanning electron microscopy–energy dispersive X-ray spectroscopy (SEM-EDS) analyses revealed the precipitation of silica nanospheres onto the surface of all the studied tissues after the first 5 h of the experiment (Figs. 1D–1F, 1J–1L). The individual silica spheres were observed to increase in size, abundance, and connectivity as the experiment proceeded (to as large as 1 μm after 116 h; Figs. 1F and 1L). Sequentially timed solution extractions show that whereas DSi concentrations decreased with time for all tested specimens, DSi concentrations remained constant for the control experiments (Fig. 2).

Potentiometric titration data were best fit by a three-site surface complexation model (i.e., three surface ligands: ≡LH, ≡XM, and ≡MH), summarized in Table S4. Titration curves are expressed relative to ultrapure water in Figures S2 and S3. Ligand ≡LH (pK_a 4.09–6.37; pK_a is the pH where 50% of a ligand is deprotonated, i.e., ≡LH and ≡L⁻) was assigned to carboxyl groups (Reaction 1 below), ≡XH (pK_a 6.41–9.10) to phosphoryl groups (Reaction 2), and ≡MH (pK_a 9.57–10.39) to either hydroxyl or amino groups, following the framework of Fein et al. (1997) (Reactions 3 and 4, respectively):
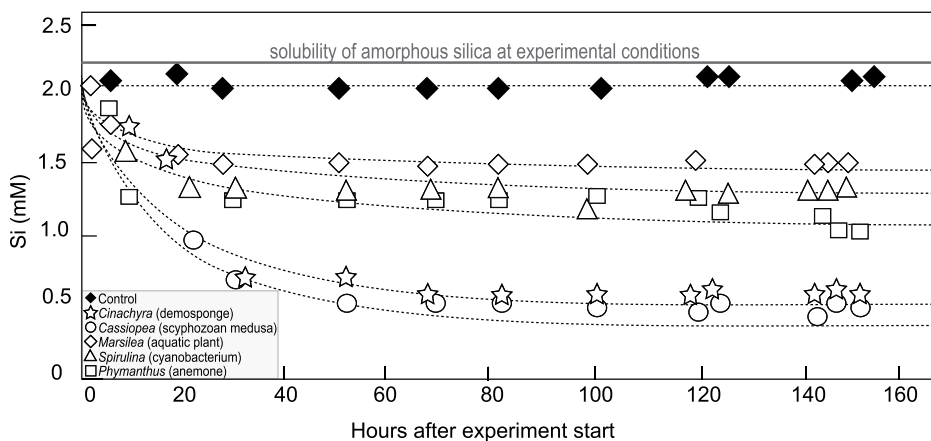
$$R\text{-}COOH + OH^- \rightarrow R\text{-}COO^- + H_2O; \quad (1)$$

$$R - PO_4H_2 + OH^- \rightarrow R - PO_4H^- + H_2O; \quad (2)$$

$$R - OH + OH^- \rightarrow R - O^- + H_2O; \quad (3)$$

$$R - NH_3^+ + OH^- \rightarrow R - NH_2 + H_2O. \quad (4)$$

Site densities are highest for ≡MH ligands, associated with amino or hydroxyl groups (Fig. 3). *Quercus* and *Marsilea* are characterized by lower site density concentrations (mean = 0.054 and 0.080 mmol/g, respectively) than the other specimens (mean = 0.15 mmol/g).

EARLY SILICA PRECIPITATION ONTO ORGANIC TISSUES

Our observations indicate that silica precipitation derived from the silica-enriched solution was facilitated by the presence of the experimental organisms. Other silica sources, such as *Cinachyra* spicules, do not appear to have contributed to experimental DSi, as indicated by their pristine preservation at the end of the experiment (Fig. S4). These results contrast with those of experiments performed by Newman et al. (2019), in which bivalve muscles were buried in coarse-grained sand, but no silica cement was observed after 45 days. Although they reported increased DSi concentrations (up to 1.5 mM) surrounding the organic tissues, this was likely due to the dissolution of kaolinite and quartz grains under low-pH conditions. Furthermore, Newman et al.'s (2019) analyses were performed at initially low DSi concentrations (0.1 mM) and acidic pH conditions (pH values of 4.5–7.5), which would have mediated decreased rates of silica polymerization (e.g., Krauskopf, 1956). In this light, the absence of silica precipitates in their experiment is unsurprising and does not indicate that silica precipitation cannot occur under the higher DSi and pH values inferred for Ediacaran oceans (Halevy and Bachan, 2017). In contrast, we provide the first report of seawater-derived silica precipitation associated with soft-bodied macroorganisms.

The amount of Si sorbed to each organism at the end of our experiments is positively correlated to its surface reactivity. Plant (*Marsilea* and *Quercus*) tissue samples were characterized by notably lower levels of silica precipitation than the other analyzed tissues (Fig. 4). Site density values are comparable to those reported by previous studies that assessed the surface reactivity of various forms of biomass (Table S4). These studies proposed three main mechanisms by which reactive organic surfaces can promote silica precipitation: (1) cation bridging between anionic ligands on the organic surface and negatively charged silica species (Phoenix et al., 2002); (2) hydrogen bonding between hydroxyl groups associated with the organic surface and hydroxyl ions of silicic acid (Phoenix et al., 2003), and (3) electrostatic interaction of cationic amino groups on organic substrates (Lalonde et al., 2005). Given that amino or hydroxyl groups (ligand ≡MH) are, in all our experiments, associated with the greatest site densities, hydrogen bonding and electrostatic interactions with amino groups offer a mechanistic explanation for the
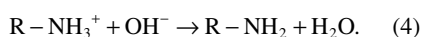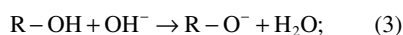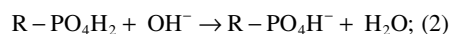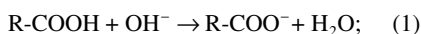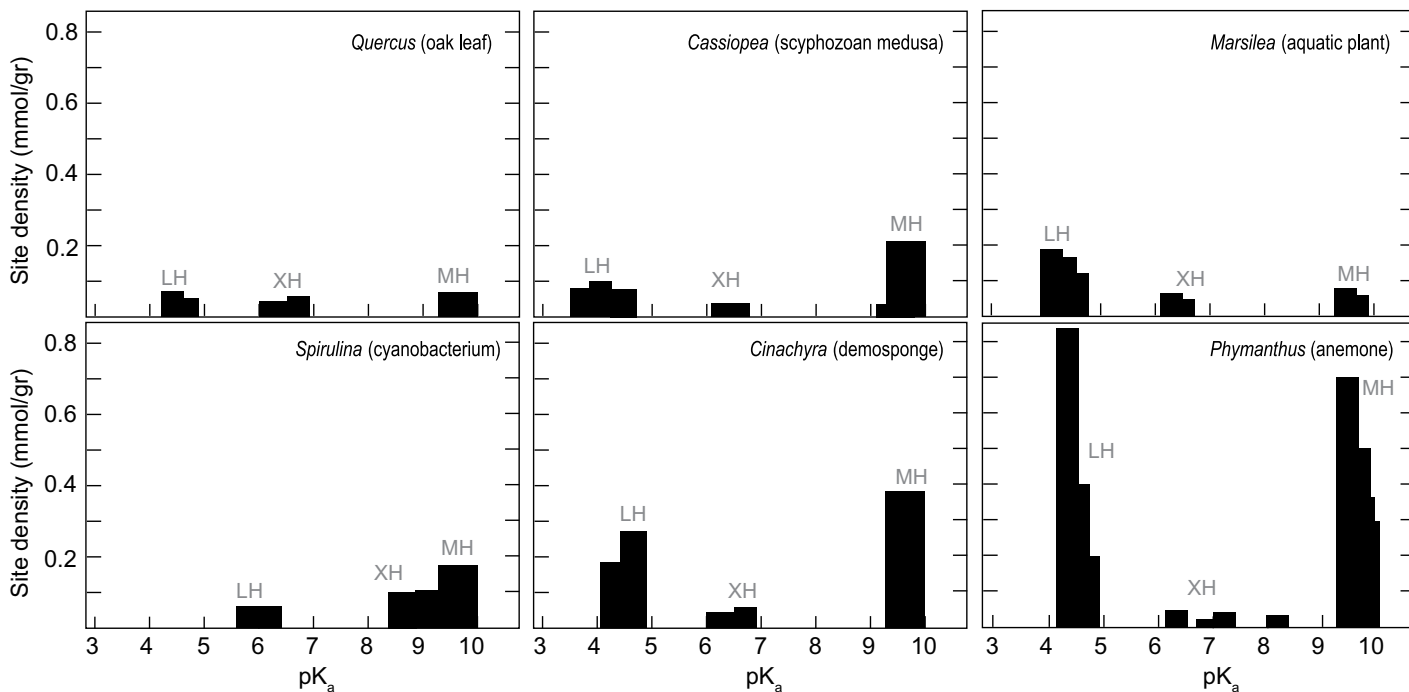

Figure 2. Si concentration plotted against time for each experiment. Each symbol is the mean of three measurements in three replicates. Standard deviations are smaller than the size of the symbols. Dotted curves are fitted by eye for comparison and do not represent any trendline fit. Solubility of silica at experimental conditions was taken from Morey et al. (1964).

Figure 3. Modeled functional groups, identified as ligands ≡LH, ≡XH, and ≡MH, of each specimen plotted as density of deprotonated sites (excess charge).

observed adsorption of negatively charged dissolved silica polymers (Parks, 1965; Iler, 1979) to organic surfaces.

The decay rate we observe is within the range of that of previous experiments performed with soft-bodied organisms, such as the anemone *Metridium* (6 days; McMahon et al., 2017). The timing of silica precipitation in our experiments closely resembles that of microorganism fossilization experiments (e.g., 24 h to 2 weeks; Oehler and Schopf, 1971). Therefore, the silica precipitation rate we observed in our experiments coincides with the optimal time frame

for the replication of external structures of soft-bodied organisms before carcass collapse and loss of surface detail.

IMPLICATIONS FOR THE RECORD OF EDIACARA-STYLE FOSSILIZATION

We observe that a wide range of soft-bodied organisms can be silicified under experimental conditions representative of Ediacaran oceans. Critically, silicification does not require the presence of recalcitrant tissues such as chitin or lignin. These results provide further refutation of the idea that Ediacara-style preservation necessi-

tates a lichen affinity for the Ediacara Biota (cf. Retallack, 1994). The early-silica-cementation model proposed by Tarhan et al. (2016) suggested that silica precipitated from DSi-enriched pore waters preferentially bonded to organic functional groups of shallowly buried macroorganisms and pervasive matgrounds, followed by continuous cementation of remaining pore space. Measured differences in silica concentrations from experimental solutions hosting organism and control samples suggest that the presence of bacterial and animal tissues shifts the silica saturation state, enhancing silica nucleation. We interpret the silica precipitation we observed in the vicinity of the experimental soft-bodied organisms to record the initial stage of fossilization responsible for exceptional "Ediacara-style" preservation by early silica cementation.

Whereas we show that silica precipitation occurs as amorphous phases, Ediacara fossils have been observed to be associated with crystalline quartz cements, occurring as syntaxial overgrowths on detrital quartz and feldspar grains (e.g., Wade, 1968; Tarhan et al., 2016). However, amorphous silica adsorbed to organic matter transforms into more crystalline silica phases by Ostwald ripening and subsequent dissolution-reprecipitation (e.g., Oehler and Schopf, 1971; Iler, 1979). Our observations show that silica precipitation—initially formed as an amorphous phase and subsequently recrystallized to quartz—is capable of proceeding rapidly enough to act as the primary agent of macrofossil preservation.

Our results do not exclude the possibility that other mineral phases, such as pyrite or clay miner-
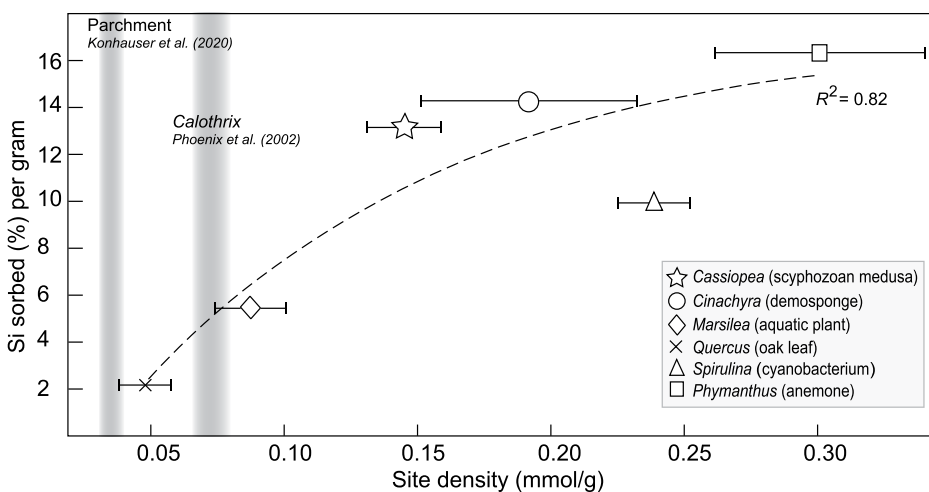

Figure 4. Mean site density (mmol/g) plotted against Si sorbed, measured at the end of the experiment (150 h) and normalized by the average weight of each specimen. Error bars represent standard deviation. Dashed line represents logarithmic trendline fit. Gray bars indicate previously reported site densities for parchment tubes of polychaete *Diopatra* (Konhauser et al., 2020) and cyanobacterium *Calothrix* (Phoenix et al., 2002).

als, may have also played a role in some instances of Ediacaran fossilization (e.g., Laflamme et al., 2011; Lui et al., 2019). However, we demonstrate that the precipitation of silica crusts onto soft-bodied organisms can easily occur under DSi concentrations and pH values reconstructed for Ediacaran seawater (cf. Siever, 1992; Halevy and Bachan, 2017). Furthermore, our experiments provide unprecedented insight into the mechanisms likely responsible for this exceptional preservation.

Further experiments exploring the relative importance of a sediment matrix and the presence of microbial matgrounds will, we hope, yield additional insights into the nature of Ediacara-style fossilization and the potential for silica bonding to organic functional groups to mediate moldic preservation in coarse quartzose sands. In light of our observations, our results further affirm that Ediacara-style fossil assemblages provide a robust archive of Earth's earliest animal communities, and that the exceptional window provided by these deposits was mediated by the high-DSi conditions of Ediacaran oceans.

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