

Exceptional preservation of soft-bodied Ediacara Biota promoted by silica-rich oceans

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ABSTRACT

The Ediacara Biota, Earth's earliest fossilized ecosystem of complex, macroscopic, multicellular organisms, occurs in terminal Ediacaran strata worldwide, yet how the fossils are preserved remains controversial. Ediacara assemblages consist of exceptionally preserved soft-bodied forms of enigmatic morphology and phylogenetic affinity. Many of these fossil assemblages are anachronistically preserved as casts and molds in sandstones ("Ediacara-style" preservation). Here we present evidence from the Ediacara Member of South Australia that Ediacara-style preservation was due to rapid, early-stage precipitation of silica cements, facilitated by the high silica saturation state of the oceans prior to the appearance of prolific silica biomineralizers. An early silicification model provides a coherent, mechanistic and empirically supported explanation for the widespread preservation of soft-bodied organisms of Ediacaran–early Paleozoic age as sandstone casts and molds. The prevalence of early silicification confirms that Ediacara-style fossil assemblages can provide an accurate window into life on the Ediacaran seafloor that can be used to reconstruct critical steps in the development and diversification of early animal ecosystems.

INTRODUCTION

Ediacaran and lower Paleozoic strata contain an unusual preponderance of soft-bodied macrofossil Lagerstätten, which are characterized by a wide range of preservational modes, from pyritization to carbonaceous compressions, phosphate or carbonate. The exceptional Ediacara-style preservation of soft-bodied organisms of the enigmatic Ediacara Biota, Earth's earliest fossilized ecosystem of complex, macroscopic, multicellular organisms, as high-relief casts and molds in sandstones (Fig. 1) in particular, has long puzzled paleontologists. In the eponymous Ediacara Member of South Australia, the beds that yield Ediacara fossils, like the fossils themselves, consist of compositionally and texturally mature, quartz-rich, fine- to coarse-grained sandstone and quartzite with an absence of mudstone or other fine-grained interbeds (Gehling and Droser, 2013). This distinctive style of fossilization is globally distributed and is particularly common among Ediacaran-aged assemblages of the Ediacara Biota (32 formation-level occurrences; Table DR1 in the GSA Data Repository¹). However, Ediacara-style preservation is not confined to either the Ediacaran Period or Ediacara Biota organisms; pre-Ediacaran (3 occurrences) and lower–middle Paleozoic (10 occurrences) examples are also known, such as quartzite-hosted assemblages from the lower Cambrian of California (USA; Hagadorn et al., 2000) and South Australia

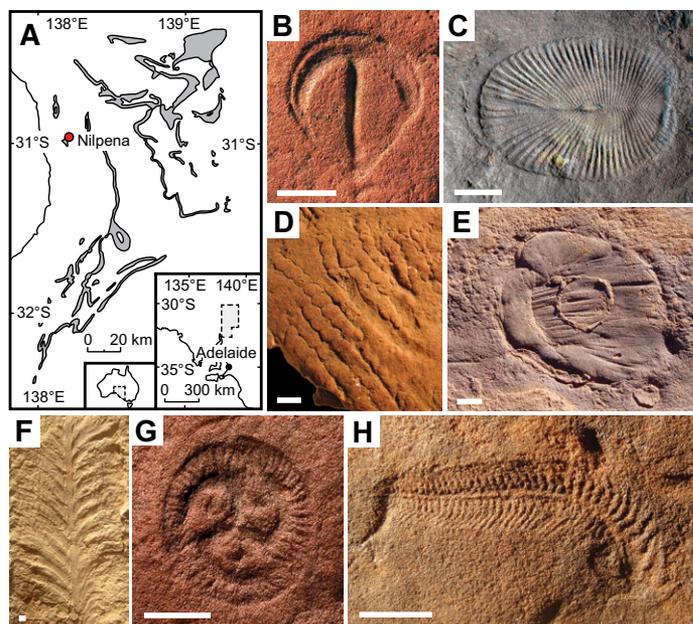


Figure 1. Ediacara-style preservation of soft-bodied organisms as sandstone casts and molds in the Ediacara Member of South Australia. This style of preservation characterizes a wide range of morphologically diverse organisms, indicating that ambient chemical conditions, rather than organismal biology, were responsible for this exceptional preservation. Scale bars = 1 cm. A: Study location in the Flinders Ranges, South Australia; gray denotes outcrop of the Ediacara Member (after Tarhan et al., 2015). B: *Parvancorina*. C: *Dickinsonia*. D: *Funisia* (South Australian Museum specimen SAM P40725). E: Current-perturbed *Aspiderella* (holdfast to a *Charniodiscus*-like frondose organism). F: *Charniodiscus* (SAM P19690a). G: *Tribrachidium* (SAM P12898). H: *Spriggina* (SAM P12771). B, C, and E are field photographs.

(Jensen et al., 1998); the middle–upper Cambrian of central and eastern North America (Collette and Hagadorn, 2010); the Ordovician of Morocco (Samuelsson et al., 2001); and the Devonian of New York (USA; Conway Morris and Grazhdankin, 2005). This taphonomic window spans hundreds of millions of years and operated independently of the phylogenetic and taxonomic affinities of the fossilized organisms.

The mechanisms responsible for Ediacara-style preservation remain enigmatic, making it difficult to gauge how faithfully these assemblages record the paleobiology and paleoecology of Ediacara ecosystems. Various preservational models have been proposed (e.g., Laflamme et al., 2011). The “death mask” model (Gehling, 1999; Liu, 2016), which posits that initial decay of microbial mats by sulfate-reducing bacteria facilitated the precipitation of a pyrite crust along the surface of the buried mat and associated macrofauna, is the most commonly invoked. This death mask subsequently served as a rigid template for the casting and molding of the

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¹GSA Data Repository item 2016325, materials and methods, analyzed specimens, petrography and composition of fossil-associated cements, stratigraphic occurrences of Ediacara-style preservation, and raw laser-ablation data, is available online at www.geosociety.org/pubs/ft2016.htm, or on request from editing@geosociety.org.

buried organisms by the surrounding sediment. However, this model is difficult to reconcile with the absence of evidence for prolific pyrite crusts or cements directly associated with Ediacara Member fossils; only late-stage (groundwater mediated) iron oxides are present along these beds (Tarhan et al., 2015). Moreover, it is improbable that either pyrite or its precursors, typically poorly crystalline spherulitic phases (Berner, 1984), could generate sufficient cement rapidly enough to promote formation of the high-relief, three-dimensional sandstone casts and molds characteristic of Ediacara-style preservation. Further, the presence of a pyrite veneer would not explain the early cementation of sand grains that is essential to the formation of sandstone casts and molds of soft-bodied organisms. Although sulfate reduction in microbial mats is pervasive through Earth's history and today, it does not typically lead to pyrite cementation of sediments.

Here we propose a new model for the preservation of Ediacara Member fossils and suggest that this model could be applicable to other Ediacara-style fossil deposits. Numerous independent lines of evidence indicate that the dissolved silica concentration of Precambrian and early Paleozoic oceans was much higher than it is today (possibly as high as 2.2 mM, near amorphous silica saturation; Konhauser et al., 2007; Siever, 1992). Modern oceans are undersaturated in dissolved silica (<0.1 mM) due to biological drawdown by silica biomineralizers such as sponges, radiolarians, and diatoms (Maliva et al., 1989). In contrast, Precambrian and lower Paleozoic sequences are characterized by an abundance of early-forming (seawater sourced) siliceous deposits, such as silicilytes and shallow-water cherts, with no post-Paleozoic or modern equivalents (Dong et al., 2015; Ramseyer et al., 2013; Shen et al., 2011). Similarly, early diagenetic silica replacement of shelly fossil assemblages and oolites has declined through the Phanerozoic (Kidder and Erwin, 2001). Whereas silica diffuses from the sediment to the overlying water column in the modern oceans (Berelson et al., 1987), during the Neoproterozoic and early Paleozoic the lack of a biogenic silica sink may have promoted diffusion of silica-rich fluids from water column to sediment (Siever, 1992), generating a taphonomic window for the early silicification of soft-bodied faunas.

Observations of modern silica-rich systems and experimental work indicate that high dissolved silica concentrations can mediate rapid silicification of organic matter, resulting in cellular-level preservation. Organic substrates provide reactive interfaces (specifically, hydrogen bond-forming carbohydrate hydroxyl groups), leading to rapid nucleation of silica films (Konhauser et al., 2001; Siever, 1992). Ediacaran and certain Paleozoic fossil assemblages characterized by Ediacara-style preservation include dense and diverse textured organic surfaces, such as dense assemblages of the tubular fossil *Funisia* (Fig. 1D), which are interpreted to record the interaction of mechanical processes with organically bound sediments, i.e., matgrounds (Gehling and Droser, 2009). Matgrounds likely provided an additional locus for rapid silicification of these assemblages.

In order to test the hypothesis that early silicification was the agent of exceptional Ediacara-style preservation, we employed a combination of paleontological, petrographic, and geochemical techniques to determine (1) the composition of cements associated with Ediacara-style macrofossils, and (2) their timing of formation. We focused on the Ediacara Member of South Australia, where the prevalence of cast and mold Ediacara-style preservation was first recognized (e.g., Glaessner and Wade, 1966). The Ediacara Member is characterized by the highest taxonomic diversity of all Ediacara Biota assemblages (Darroch et al., 2015), and preserves considerable breadth in fossil morphology and sedimentary facies (Gehling and Droser, 2013). Systematic excavation at Nilpena Station, on the western margin of the Flinders Ranges (Fig. 1A), has allowed reconstruction of hundreds of square meters of Ediacara bedding planes, facilitating detailed paleoecological and taphonomic characterization of in situ fossil assemblages. The taphonomy and sedimentology of Ediacara macrofossils and textured organic surfaces were documented at the scales of assemblages, beds, and individuals. Fossil samples were also collected for petrographic and geochemical analyses.

RESULTS

The soft-bodied macrofossils of the Ediacara Member are preserved by casting and molding of millimeter-scale features by fine- to coarse-grained sandstone (Fig. 1). Macrofossils are three-dimensional and characterized by high (millimeter- to centimeter-scale) relief; textured organic surfaces are similarly preserved. This high-fidelity preservation is present across a wide range of morphologies, paleoecologies, and sedimentary facies (Fig. 1), indicating that sandstone cementation occurred prior to extensive tissue degradation on a broad, biota-wide scale.

Ediacara fossils are preserved as three-dimensional casts and molds along and within silica-cemented quartzofeldspathic arenite beds (Fig. 2). Macrofossil-associated sandstone porosity has been occluded almost entirely by authigenic silica cements (Fig. 2). Other diagenetic precipitates, such as clays, iron oxides, and carbonates, are relatively rare and commonly late stage (e.g., associated with fractures) (Figs. 2D–2H). Even where sedimentary laminae are finer grained, clay minerals and oxides are not preferentially associated with Ediacara fossils. Cathodoluminescence (CL) microscopy (Figs. 2 and 3) reveals that detrital quartz and feldspar grains rarely contact, and are commonly bounded by nonluminescent, syntaxial silica overgrowths in optical continuity with host grains (cf. McBride, 1989). Feldspar grains rarely show feldspar overgrowths, but are commonly abutted by authigenic quartz cements, which appear to have largely outcompeted the feldspar rims. Samples are characterized by a paucity of dissolution or pressure solution features such as microstylolites or concave-convex grain contacts (cf. Pittman, 1972). The pervasive presence of silica cements, which filled nearly the entirety of available pore space prior to compaction, indicates that they precipitated at an early diagenetic stage (due to continuous cementation, petrographic data constrain burial depth only to <1–2 km; cf. Sibley and Blatt, 1976; however, paleontological evidence points to the shallowest end of this range). Thus, petrographic (light, scanning electron, and CL microscopy) and compositional (energy-dispersive X-ray spectroscopy and microprobe) analyses provide compelling evidence that silica cements formed early in the diagenetic history of these assemblages.

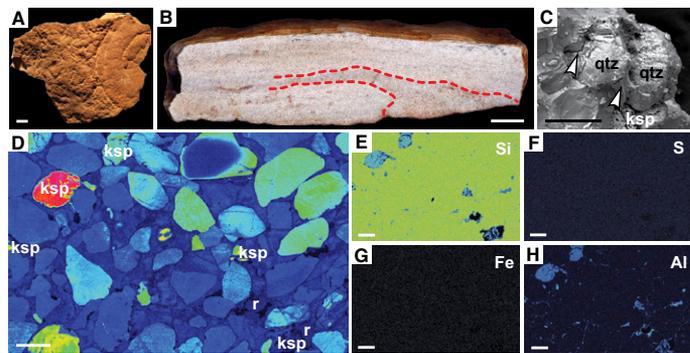


Figure 2. Petrographic and compositional characterization of silica cements associated with three-dimensionally preserved *Aspidella* holdfast and entrained stalk (A,B: South Australian Museum specimen SAM P50846; outlined by dashed lines in B). C: Backscattered electron image of porosity-occluding early silica cements (arrows) nucleated around detrital quartz grains (qtz; ksp—k-feldspar). D: Cathodoluminescence brightness map of authigenic silica-cemented detrital quartz and (labeled) ksp grains associated with *Aspidella* holdfast (in A and B). Areas labeled r are resin-impregnated holes. E–H: Energy dispersive spectroscopy (EDS) elemental maps of same area as shown in D. EDS maps indicate that fossils are associated with enrichments in silicon (Si), limited aluminum (Al); largely associated with detrital feldspar grains and late-stage authigenic clay), and a paucity of iron (Fe) or sulfur (S). Relative abundance is denoted by distribution and brightness of color. Black areas in E are resin-impregnated holes in sandstone matrix. Scale bars: A, B = 1 cm; C–H = 100 μ m.

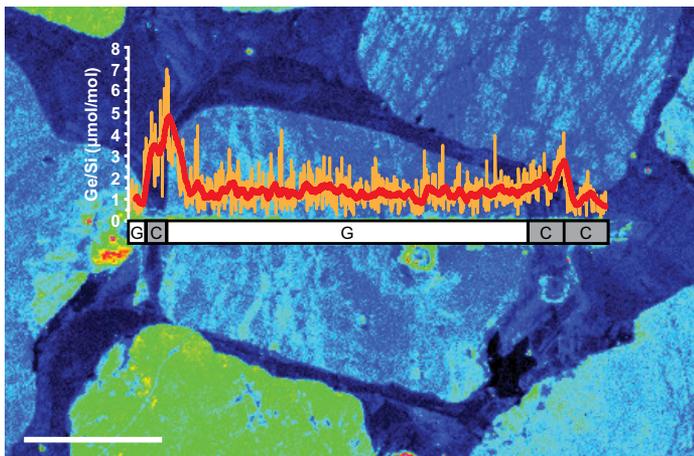


Figure 3. Geochemical characterization of macrofossil-associated silica cements. Ge/Si ($\mu\text{mol/mol}$) ratios, generated by laser ablation–inductively coupled plasma–mass spectrometry (LA-ICP-MS) (Ge) and microprobe analyses (Si), plotted as overlay on cathodoluminescence brightness map of ablated area, indicate that silica cements associated with Ediacara macrofossil *Wigwamiella* (South Australian Museum specimen SAM P54194) are characterized by significantly higher Ge/Si values than adjacent detrital quartz sand grains. Ge data were collected sequentially via continuous horizontal LA. Outliers were rejected at the ± 3 standard deviation level. Yellow curve denotes raw data; red curve denotes moving average (period = 15 points). LA-ICP-MS protocol error <0.37%; spot size 19 μm . G—grain; C—cement. Scale bar = 100 μm . Raw data compiled under 18A_L11 in Table DR2 (see footnote 1).

The ratio of germanium (Ge) to silicon (Si) also provides a means by which to test whether Ediacara silica cements are late stage (as is typical of silica-cemented sandstones; cf. McBride, 1989) or early diagenetic in origin (cf. Hamade et al., 2003). Ge commonly substitutes for Si (in trace quantities) in silicate minerals at a Ge/Si ratio reflecting the environment of precipitation (Bernstein, 1985). Cements precipitated during high-temperature or high-pressure dissolution-precipitation reactions (i.e., late diagenetic remobilization of grain-bound silica) would be characterized by Ge/Si values equal to or lower than grain Ge/Si values (Evans and Derry, 2002). Micron-scale laser ablation–inductively coupled plasma–mass spectrometry indicates that silica cements sampled directly from and

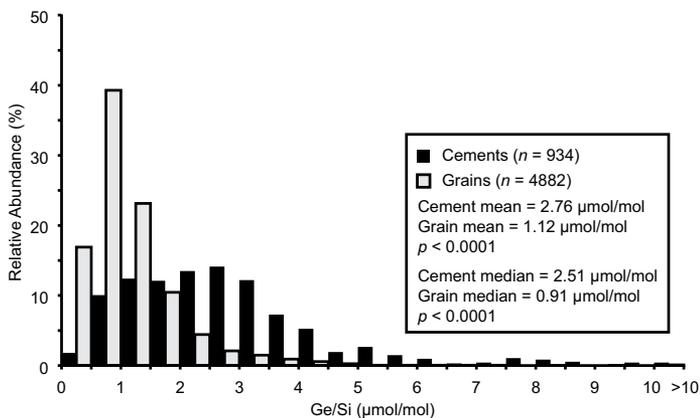


Figure 4. Size-frequency distribution of Ge/Si ($\mu\text{mol/mol}$) values of all analyzed silica cements and grains. Cements and grains are characterized by statistically robust disparity in Ge/Si values. Mann-Whitney U (median) and Monte-Carlo (mean) p -values denote the probability that cement and grain values are significantly different ($p < 0.05$ denotes significant differences). See Table DR2 (see footnote 1) for raw data.

within millimeters of Ediacara fossils are characterized by Ge/Si values significantly disparate from the surrounding detrital quartz sand grains [median cement Ge/Si = 2.51 $\mu\text{mol/mol}$ ($n = 934$) versus median grain Ge/Si = 0.91 $\mu\text{mol/mol}$ ($n = 4882$); Figs. 3 and 4; Table DR2]. This trend is statistically robust across all analyzed specimens (Monte Carlo and Mann-Whitney U tests both <0.0001). Thus Ediacara cement Ge/Si ratios indicate a non-grain source for cement silica, bolstering the case for early silicification. Furthermore, the Ediacara Member contains no evidence for hydrothermal activity and Ediacara cement Ge/Si values are below the range typically associated with hydrothermal or high-temperature fluids (8–14 $\mu\text{mol/mol}$; Mortlock et al., 1993) and do not covary systematically with rim thickness. The fossiliferous Ediacara Member consists of tens to hundreds of meters of quartzofeldspathic arenite and is bracketed by hundreds of meters of lithologically similar material (Gehling and Droser, 2013). Significant differences in cement Ge/Si between disparate fossil taxa, stratigraphic horizons, lithofacies, and localities were not observed (see Table DR2), in contrast to the spread in values predicted for a system characterized by long-range fluid transport and precipitation, given Ge/Si fractionation during cement formation (Evans and Derry, 2002). Early silica cementation thus offers the most parsimonious explanation for observed cement geochemistry.

DISCUSSION

Early Silicification: A Taphonomic Model

Ediacara Member macrofossils are characterized by taphonomic, petrographic, and geochemical evidence for pervasive, early-forming silica cements, and a paucity of iron-, clay-, or carbonate-rich phases. These data indicate that early diagenetic precipitation of silica cements was critical to the exceptional three-dimensional preservation of these fossils in sandstone. We propose the following taphonomic sequence: death and burial of Ediacara communities were followed by rapid nucleation of silica films on macroorganisms and matgrounds and precipitation in the surrounding pore space, facilitated by preferential bonding of seawater-derived silica to organic functional groups (cf. Konhauser et al., 2001). Early and continuous silica cementation permitted the sand grains molding the buried soft-bodied organisms to gain sufficient coherence to form detailed, high-relief casts and molds before decay resulted in carcass collapse and loss of surface detail. Silicification was not sufficiently rapid and/or pervasive to facilitate carcass chertification, which is exceedingly rare in mature sandstones of any age. Elevated cement Ge/Si values may reflect organophile behavior of Ge, which can be sorbed onto organic matter and subsequently released to pore waters, resulting in high Ge/Si pore-water values (Pokrovski and Schott, 1998) that can be captured by early-forming silica cements.

Implications for the Evolution of Early Animals and the Global Silica Cycle

The temporal window of Ediacara-style fossilization is bracketed both locally (field observations indicate that early silica cementation is common throughout the Adelaide Fold Belt, from the Tonian Burra Group to the Cambrian Ajax Limestone) and globally (Dong et al., 2015; Kidder and Tomescu, 2016; Ramseyer et al., 2013; Shen et al., 2011) by anactually high marine dissolved silica concentrations during the Precambrian and early Paleozoic, as evidenced by a range of sedimentological, geochemical, geobiological, and paleontological data. This taphonomic window persisted across the Precambrian-Cambrian boundary and also characterizes Paleozoic fossil assemblages of crown-group animals, indicating that the paleobiology and evolutionary longevity of the Ediacara Biota was not a major driver of Ediacara-style preservation. Moreover, the decline of Ediacara-style preservation (in the early–middle Paleozoic) coincided with the radiation of siliceous sponges and, in particular, radiolarians, likely the major silica biomineralizers (and thus silica

sinks) until the rise of diatoms (Kidder and Tomescu, 2016). Closure of the Ediacara-style preservational window may therefore reflect global-scale evolution of the marine silica cycle and, in particular, the advent of biological silica cycling.

Although our data constrain the diagenetic history of a single unit, the Ediacara Member records the operation of taphonomic processes controlled by global-scale biogeochemical conditions. Therefore, although other taphonomic processes may have contributed elsewhere, early silicification appears to have played an important role in the preservation of other Ediacara-style fossil assemblages. Evidence for early silicification across a wide range of tissue types demonstrates the importance of a global and persistent environmental control on fossilization, i.e., high marine silica concentration. Resolving this long-standing taphonomic paradox allows genuine evolutionary signals (e.g., extinction events) to be distinguished from preservational artifacts. An early silicification taphonomic model indicates that the geologically abrupt appearance and subsequent disappearance of the Ediacara Biota is a valid evolutionary signal. It also provides the first empirical support for the contention that Ediacara-style fossil assemblages truly reflect the diversity, trophic complexity, and community-level ecology of Earth's oldest fossil animal ecosystems.

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