Depositional and preservational environments of the Ediacara Member, Rawnsley Quartzite (South Australia): Assessment of paleoenvironmental proxies and the timing of 'ferruginization'

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ABSTRACT

The paleoenvironmental setting in which the Ediacara Biota lived, died and was preserved in the eponymous Ediacara Member of the Rawnsley Quartzite of South Australia is an issue of longstanding interest and recent debate. Over the past few decades, interpretations have ranged from deep marine to shelfal to intertidal to terrestrial. Here we examine the evidence in support of and against various paleoenvironmental interpretations of the fossiliferous Ediacara Member, as well as exploring in depth a range of paleoenvironmental proxies that have historically been employed in such studies. We emphasize the importance of reconciling paleoenvironmental analysis with an understanding of sedimentological processes and outline which proxies are consistent with this approach. A careful assessment of paleoenvironmental parameters is essential to the reconstruction of the depositional and early diagenetic history of the Ediacara Biota and thus the physical, chemical and biological factors that shaped the development and the fossilization of these earliest examples of complex life. We find no compelling evidence for a terrestrial setting for the Ediacara Member and strong support for a shallow marine depositional environment.

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1. Introduction

The well-known fossils of the Ediacara Biota, which record Earth's earliest complex, macroscopic communities, occur in the eponymous Ediacara Member of South Australia (Figs. 1–2). Depositional models for the fossiliferous Ediacara Member have, historically, covered the gamut of marine and marginal marine settings. Jenkins et al. (1983), for instance, suggested deposition in a lagoonal and barrier-bar system. However, further mapping of the contact between the Ediacara Member and the underlying Chace Quartzite Member of the Rawnsley Quartzite has revealed an erosional unconformity formed by an Ediacaran incisional event which subsequently produced greater accommodation space and led to deeper-water, storm-mediated deposition, followed by shallow-water shelfal and delta-front progradation (Gehling, 1982, 2000; Gehling and Droser, 2012). Previous interpretations of an intertidal origin for the fossiliferous Ediacara Member have historically relied largely on features interpreted as mud cracks (Jenkins et al., 1983), subsequently reinterpreted as synersis cracks occurring in tempestite-dominated facies entirely devoid of mud (Gehling, 2000). Subsequent detailed sedimentological analysis has indicated that Ediacara fossils occur primarily in four separate facies of the Ediacara Member, recently demarcated as the "Wave-Base Sandstone Facies," "Delta-Front Sandstone Facies," "Sheet-Flow Sandstone Facies" and "Mass-Flow Sandstone Facies" (Gehling and Droser, 2013). Ediacara fossils are rarely found in a fifth facies, the "Shoreface Sandstone Facies" and are entirely absent from the more marginal marine and floodplain facies typical of the underlying Chace Quartzite Member ("Intertidal Mat Sandstone Facies") and Bonney Sandstone ("Fluvial Deltaic Sandstone Facies") (Gehling and Droser, 2013).

In contrast, recent studies (Retallack, 2013) have claimed a terrestrial origin for the fossiliferous Ediacara Member. This model, which is based on interpretations of geochemical and sedimentological data from putative paleosol horizons along which Ediacara fossils are also preserved (Retallack, 2012, 2013), is intriguing in light of the long-prevailing interpretation that these successions were formed through deposition of sediments under marine conditions. Correct identification of paleosols in the sedimentary record is a difficult task and one that has long challenged geologists. In particular, paleosols preserved in successions older than the mid-Paleozoic, prior to the widespread establishment of vascular land plants, record anactualistic settings and therefore present a not insignificant challenge to traditional, uniformitarian-guided paleoenvironmental assessment. However, the striking dichotomy between these two schools of paleoenvironmental reconstruction indicate, more fundamentally, a profound disagreement in the selection and interpretation of paleoenvironmental proxies. We therefore, using the Ediacara Member as a case study, examine the various approaches and techniques that

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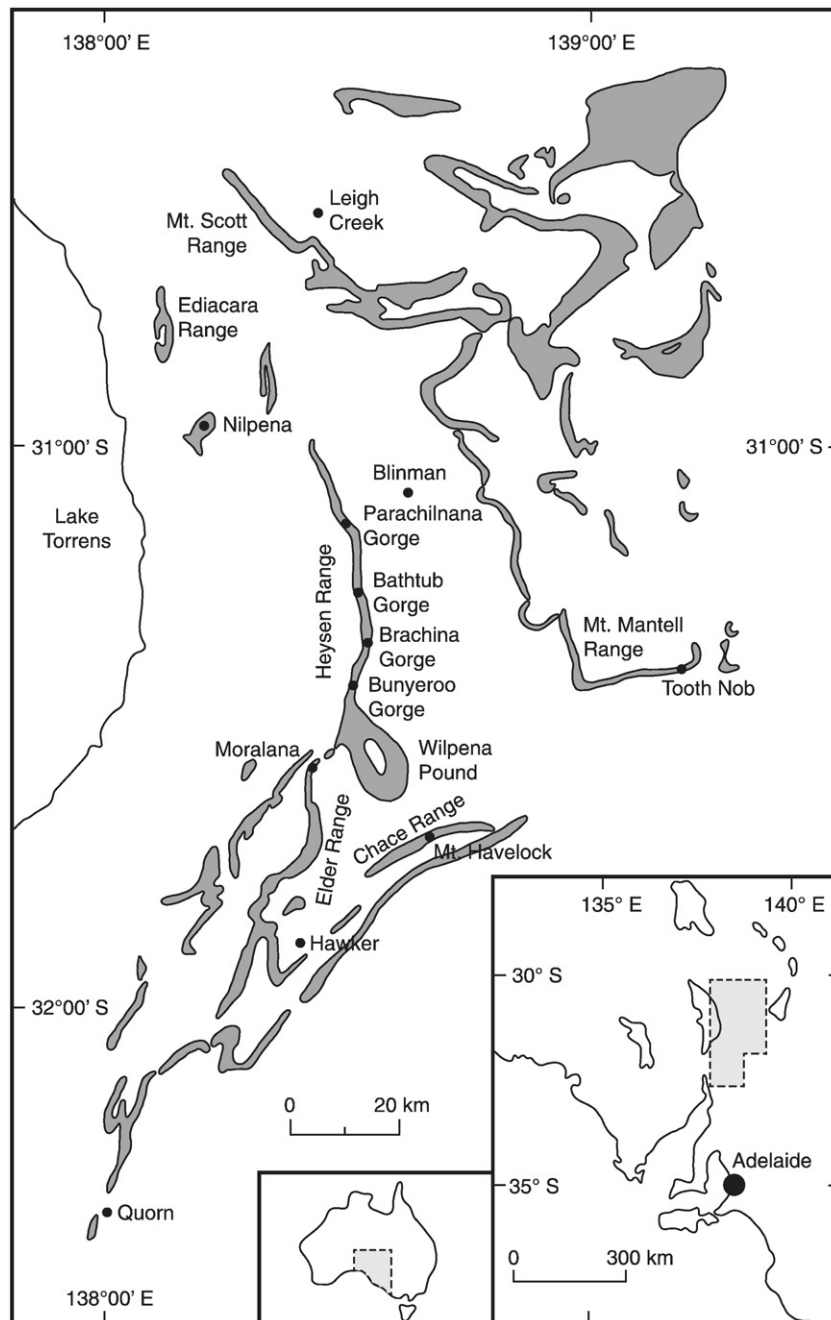 E-mail address: lidya.tarhan@yale.edu (L.G. Tarhan).

Fig. 1. Geographic context of Ediacara fossil deposits of the Flinders Ranges of South Australia. Modified from Tarhan et al. (2015).

have been employed as proxies for Ediacara paleoenvironments, and assess the strengths, weaknesses and utility of each in turn. Ultimately, we contend that the arguments presented by Retallack (2012, 2013) for a terrestrial origin of these fossils are not consistent with a process-oriented analysis of the sedimentology of these deposits, whereas reconstruction of the fossiliferous facies of the Ediacara Member as a shallow marine system is much more strongly and parsimoniously supported.

2. Sedimentology, geochemistry and paleontology of the Ediacara Member

2.1. General sedimentology

Twenty-seven fossiliferous beds of the Ediacara Member have, to date, been excavated and serially reconstructed at the National Heritage-listed Ediacara fossil sites at Nilpena and the Ediacara Conservation Park in South Australia (Fig. 1). Ediacara fossils occur in dense and compositionally heterogeneous assemblages as part and counterpart impressions on the tops and corresponding bases of thin to medium (cm- to dm-scale), rippled, well-sorted, medium- to coarse-grained feldspathic quartz sandstone beds (Figs. 2–3). Twenty-three of the fossiliferous beds are rippled (e.g. Fig. 3A) and most are further characterized by preservation of textured organic surfaces (TOS), which overprint and mute ripple crests and troughs (Gehling and Droser, 2009). Moreover, sedimentological analysis of two recently excavated fossiliferous horizons reveals surfaces characterized by prominent and well-preserved symmetrical ripples, indicative of oscillatory flow. The presence of multiple generations of in situ fossils and well-developed TOS on these bedding planes strongly suggests that these communities persisted over relatively long periods of time in an environment of active oscillatory flow. Combined-flow ripples
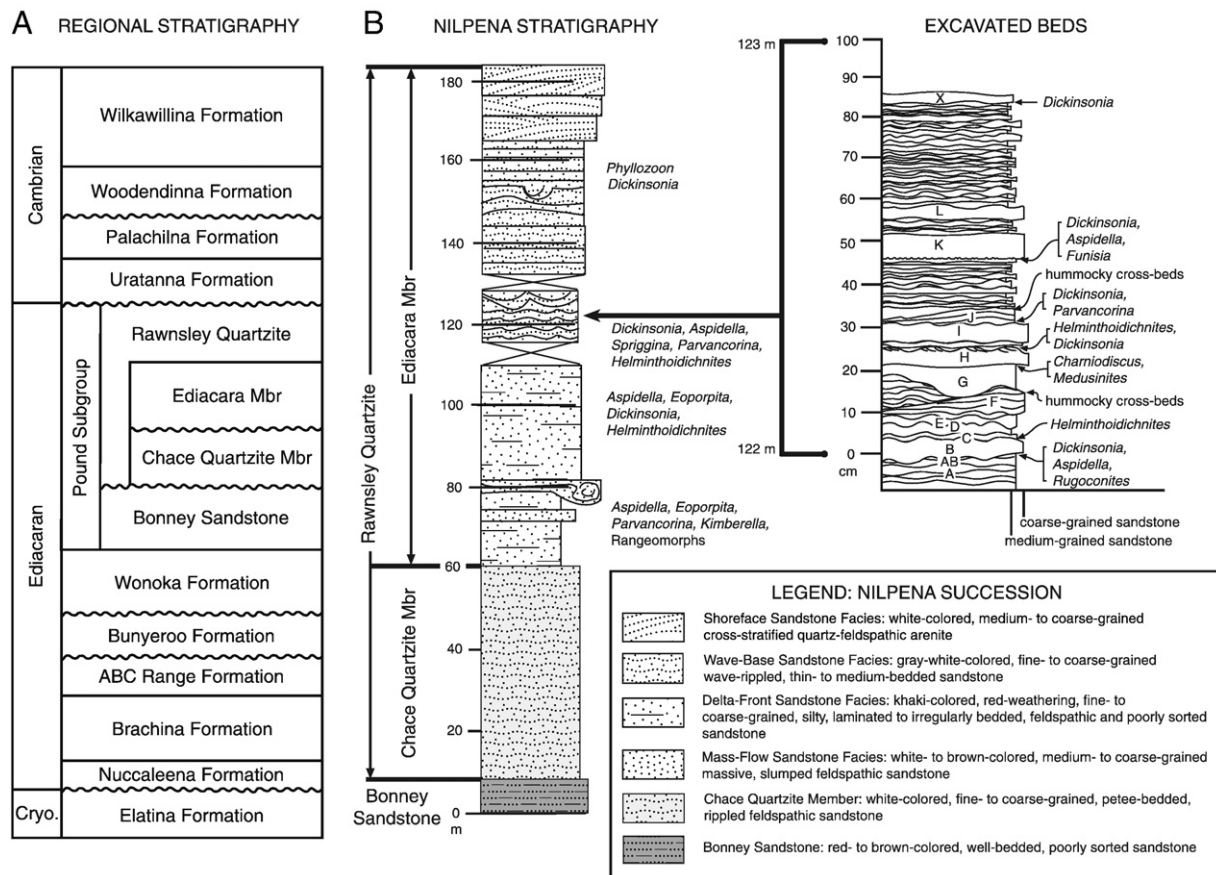
Fig. 2. Regional (A) and local (B) stratigraphic context of Ediacara fossil deposits at Nilpena (Flinders Ranges, South Australia). Ediacara fossils occur in a wide range of facies recording deposition in shallow marine paleoenvironments.
Modified from Tarhan et al. (2015).

are also abundant (e.g. Fig. 3B). Moreover, the strong correspondence of particular fossil assemblages to particular marine facies across globally-distributed Ediacaran-aged deposits characterized by disparate lithofacies most parsimoniously indicates that the Ediacara fossils are marine in origin. Specifically, the global and likely marine distribution of the Ediacara Biota is supported by correlation of the South Australian fossil assemblages (wave-rippled sandstone) with those of the White Sea region of Russia (interbedded sandstone and siltstone) and with taxa common in Ediacaran successions of Namibia (lenticular sandstone) and Newfoundland (siltstone and fine-grained sandstone), as well as recent discoveries of taxa shared by the Ediacara Member and the Doushantuo Formation of South China (black shale) (Grazhdankin, 2004; Zhu et al., 2008; Narbonne et al., 2009; Gehling and Droser, 2012, 2013; Xiao et al., 2013). Therefore, a broad suite of sedimentological and facies indicators of the Ediacara Member points strongly to a subaqueous, shallow marine benthic habitat characterized by oscillatory and storm-mediated flow and suggests that these were conditions experienced by multiple generations of Ediacara communities. To overlook these features in making a paleoenvironmental interpretation is scientifically unsound. To interpret these features as the result of desiccation and terrestrialization of a formerly subaqueous, marine system is—particularly in the absence of any desiccation features such as mud cracks or salt hoppers—unparsimonious.

2.2. Color, weathering and provenance

The ruddy color of certain fossiliferous sedimentary packages of the Ediacara Member has been a central tenet in previous interpretations of a terrestrial origin for Ediacara fossil assemblages. However, color is not an accurate metric of the depositional history of these rocks but instead reflects the present-day ferric iron content of the Ediacara succession.

Color thus cannot be considered diagnostic of a terrestrial, or even a synsedimentary origin of iron oxides. Once all of the organic content or later-stage diagenetic pyrite of a sedimentary unit is oxidized, color is almost entirely determined by the redox state of thin coatings of iron hydroxides, which can oxidize or reduce multiple times during diagenesis (Myrow, 1990). Simply put, ferrous iron may be subsequently oxidized by diagenetic fluids; the possibility of supergene or late-stage diagenetic alteration cannot be ruled out on the basis of color. In most cases, the color red is thus not directly correlated to the degree of syndepositional weathering a particular succession has experienced, but rather simply reflects the present-day ferric iron content of the constituent rocks (or outcrop landscape). The extent to which different units of a succession are oxidized may largely reflect the inherent sedimentological properties of each unit. The coloration of the fossiliferous Ediacara Member at Nilpena, for instance, strongly reflects post-depositional, late-stage processes. Iron staining at Nilpena is prevalent but largely surficial and does not follow bedforms (Fig. 4); red coloration is patchy (Fig. 4A–B, D–G) and non-penetrative (Fig. 4C) and demonstrably late-stage features such as Liesegang banding are not uncommon in Ediacara successions, both at Nilpena and elsewhere throughout the Flinders Ranges.

This applies equally to surficially exposed outcrops and to strata buried hundreds of meters beneath the surface—particularly the subsurface of Australia (Li et al., 2012). For instance, deep drill core samples of Archean-aged strata from the Pilbara Craton of northwestern Australia record evidence of late-stage (Phanerozoic-aged) oxic alteration, in spite of the fact that these strata are interbedded with non-oxidized facies (Li et al., 2012). In the case of the Pilbara Craton, late-stage alteration clearly does not impact all intervals of a succession uniformly, nor even necessarily gradationally. Oxidation may be diagenetic and yet
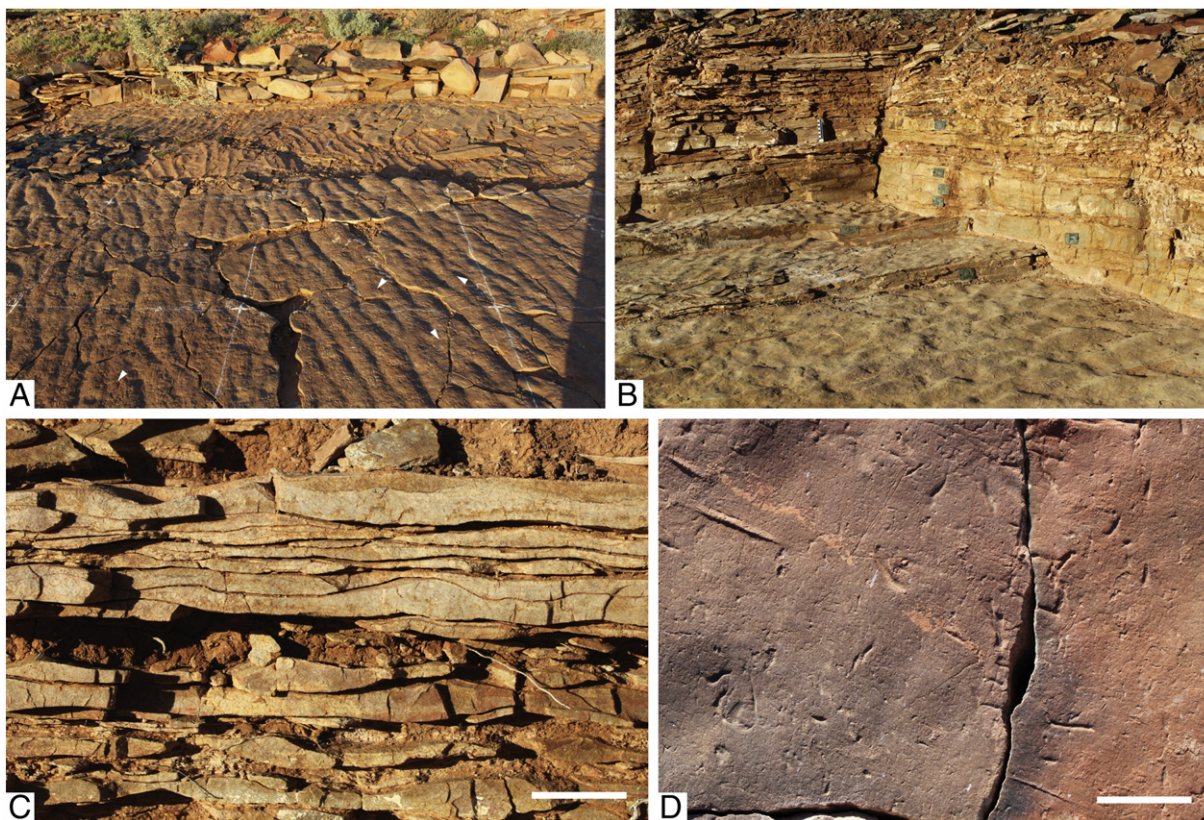
Fig. 3. Sedimentology of the Ediacara Member at Nilpena, South Australia. (A)–(C) Sedimentology and stratigraphic context of the fossiliferous Wave-Base Sandstone Facies. (A) Fossiliferous horizon characterized by oscillatory ripples and dense assemblages of *Aspidella* (e.g. see arrows) and *Funisia*. Hyporelief. Chalk marks denote 1 m × 1 m grids. (B) Quarry containing sequentially excavated beds (labeled with metal plaques) of the Wave-Base Sandstone Facies. Each bed base is characterized by a dense, diverse and disparate assemblage of Ediacara fossils and textured organic surfaces (TOS); sequential beds are characterized by strong paleoecological heterogeneity. Epirelief. Figured scale bar is 10 cm. (C) Cross-sectional view of oscillatory ripples of the Wave-Base Sandstone Facies. (D) Sedimentology of fossiliferous beds of the Sheet-Flow Sandstone Facies. Fossiliferous beds are characterized by planar lamination and crisply preserved tool marks. Hyporelief. Scale bars (C–D) = 5 cm.

may be bedding-plane parallel or may characterize only certain beds in a succession. There is no reason to assume that the interbedding of oxidized and non-oxidized units axiomatically requires a syndepositional, let alone terrestrial origin for the former. Neither the alternation of red and non-red rocks, nor the concurrent deposition of red and non-red intraclasts is a diagnostic indicator of a terrestrial origin for the red strata; color banding is therefore insufficient evidence for "synsedimentary ferruginization," as invoked by Retallack (2012, 2013) for the Ediacara Member. Diagenetic oxidation may be guided not only by inherent sedimentological properties of a rock, but also, not surprisingly, by the occurrence of deformational features such as faults or joints. The Ediacara Member of Brachina Gorge, for instance, from which samples interpreted as paleosols have previously been collected (e.g. Retallack, 2012), is extensively fractured and faulted (e.g. Fig. 4E; Gehling and Droser, 2012; Retallack, 2012); it is therefore not unlikely that post-depositional fluid flow has influenced the late diagenetic history of these strata. Likewise, neither the presence of reworked clasts nor their coloration can provide a uniquely terrestrial paleoenvironmental signature. Storm-mediated reworking of cohesive or cemented seafloor sediments (e.g. matgrounds, firmgrounds or hardgrounds) is a common phenomenon throughout the geologic record and has, moreover, been observed to have been particularly common in Neoproterozoic–lower Paleozoic successions and has been linked to both a higher preponderance of organically-bound substrates and lower intensities of bioturbation during this interval (e.g. Sepkoski et al., 1991). Given that the Ediacaran substrate is commonly interpreted, based on a broad range of sedimentological and paleontological evidence from Ediacaran successions worldwide, to have been characterized by widespread microbial mats and biofilms (Gehling, 1999; Gehling and Droser, 2009), it is not surprising that the Ediacaran stratigraphic record is characterized by

abundant reworked clasts, particularly in environments characterized by oscillatory and storm-mediated current flow.

Further, there are numerous examples throughout the rock record of marine successions characterized by alternating red and non-red strata with clear sedimentological and fossil evidence for a marine depositional setting, such as the trilobite-rich lower Cambrian Latham Shale of California (e.g. Briggs and Mount, 1982; Moore and Lieberman, 2009) and Ediacaran–Cambrian successions of Avalonia (Crimes and Anderson, 1985; Callow et al., 2013). It is therefore not parsimonious to interpret, as has been recently done (Retallack, 2012, 2013), the mere alternation of red and non-red strata as evidence of a terrestrial origin for the former. As important, even assuming a primary origin for the ferric iron, the presence of iron-rich sediment and variations in ferric-ferrous iron ratios are not diagnostic of any particular depositional environment. Iron-rich sediments are not exclusively terrestrial; sediment deposited in a marine setting may be rich in either ferric or ferrous iron (e.g. Canfield, 1989).

2.3. Carbonate nodules and nodule geochemistry

Carbonate nodules have also been mooted as evidence for a paleosol origin for Ediacara strata (Retallack, 2012, 2013). However, carbonate nodules are by no means an exclusively terrestrial, intra-soil phenomenon; their occurrence along particular horizons does not diagnostically indicate a particular paleoenvironmental origin for either the nodules or the host sediments. Either marine or terrestrial successions may contain distinct horizons of nodules. In fact, as recently noted (Xiao and Knauth, 2013), early- to meso-diagenetic nodules are a common component of not only terrestrial, but also marine successions (e.g. Irwin et al., 1977; Coleman and Raiswell, 1981; Burns and Baker, 1987).
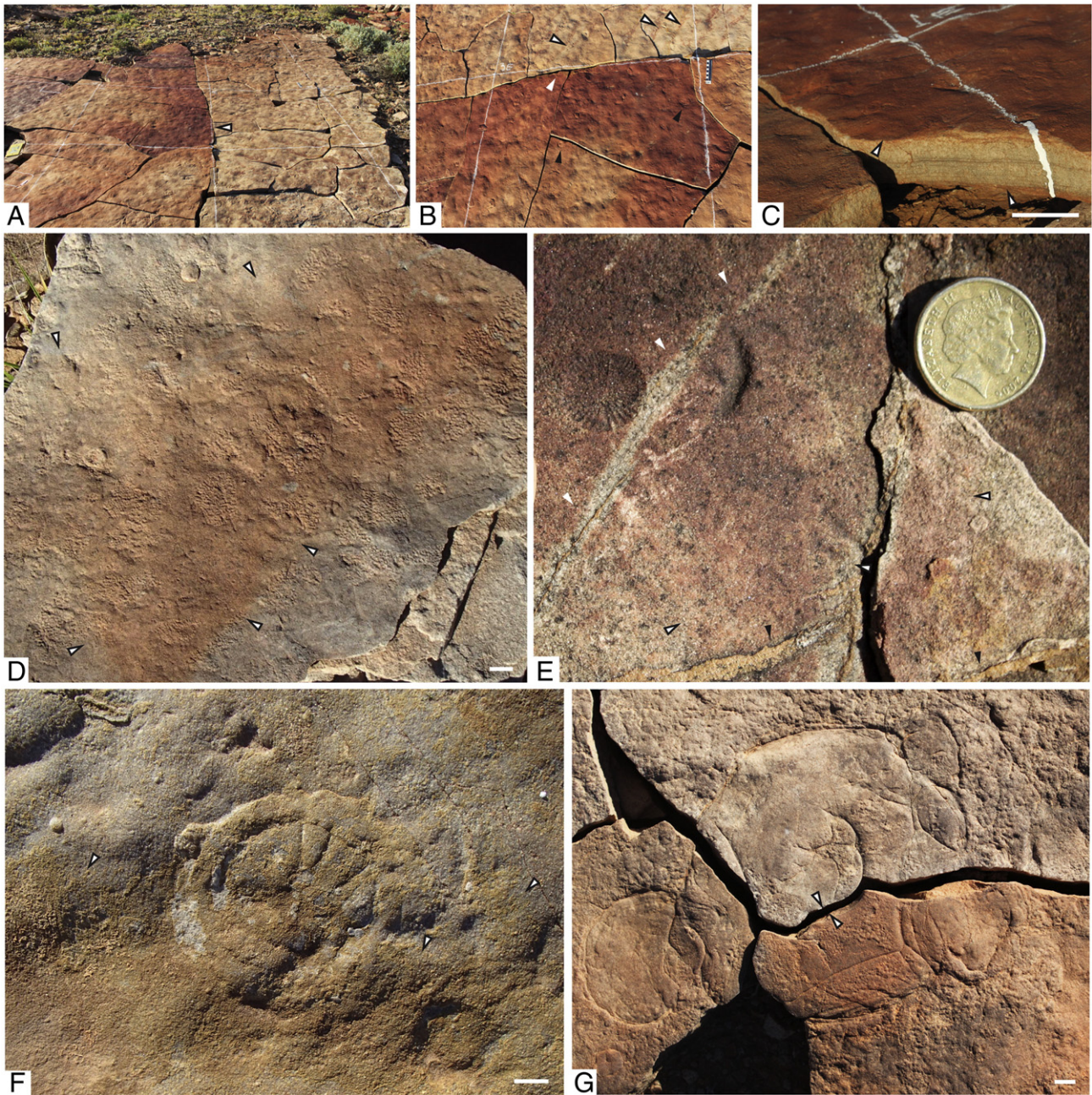
Fig. 4. Ferric iron in the Ediacara Member. Fossiliferous beds of the Ediacara Member are commonly iron-stained; these iron stains are characterized by irregular, patchy spatial distribution along bedding planes (A–B, D–G) and lack of intra-bed penetration (C). Note abrupt and irregular junctions between bright red iron-stained surfaces and non-red surfaces (black-rimmed white arrows in [A], [D], [E], [F] and [G]; white arrow in [B]). (A–C) Sandstone bedding plane (Wave-Base Sandstone Facies) dominated by the biogenic tool mark "mop" (black arrows in [B]). (B) Iron staining is also concentrated along oscillatory ripple crests (negative-relief 'troughs' on base of figured counterpart bed; see black-rimmed white arrows). (C) Iron staining is surficial and does not penetrate beyond bed partings (black-rimmed white arrows). Hyporelief (A–B) and cross-section (C). (D) Sandstone surface (Sheet-Flow Sandstone Facies) characterized by irregular iron staining and dense clusters of the textured organic surface (TOS) "micropucker." Hyporelief. (E) Sandstone bedding plane (Delta-Front Sandstone Facies) characterized by *Dickinsonia*, irregular iron staining (black-rimmed white arrows), crack-associated discoloration (white arrows) and infilled veins (black arrows). Hyporelief. (F) *Wigwamiella* on sandstone bedding plane (Wave-Base Sandstone Facies) characterized by irregular iron staining (black-rimmed white arrows). Hyporelief. STC-H-02. (G) *Aspidella* on sandstone bedding plane (Sheet-Flow Sandstone Facies) dominated by *Aspidella* fossil assemblages, dense surface coverage of *Funisia* TOS and irregular coloration on both the bedding-plane and individual fossil scale. Hyporelief. MASP-04. Nilpena (A–D, F–G) and Brachina Gorge (E). Chalk marks (A–C) denote 1 m × 1 m grids; figured scale bars (A–B) are 10 cm long; Australian one-dollar coin (E) is 2.5 cm in diameter; white scale bars (C–D, F–G) are 1 cm long.

Additionally, depleted isotopic (δ^{13}C and δ^{18}O) signatures are not diagnostic of a terrestrial setting for nodule formation. Since the carbon in marine nodules is typically sourced from remineralized sedimentary organic matter, not the marine DIC reservoir, marine nodules are typically characterized by isotopically light carbonate carbon isotope values. Alternatively, isotopically light carbonate carbon values in marine strata may be linked to late-stage diagenesis (e.g. Derry, 2010). Likewise,

oxygen isotopes have long been known to be extremely prone to diagenetic alteration and therefore, particularly in rocks of Neoproterozoic age, cannot be confidently interpreted to unequivocally record the primary composition of either precipitation or seawater, at least not without employing additional indices to assess degree of alteration. In fact, correlation between carbon and oxygen isotopes has long been taken as an indication that diagenetic alteration has occurred

(e.g. Marshall, 1992; Derry, 2010). Therefore, in the case of the Ediacara Member, the presence of carbonate nodules characterized by light carbon and oxygen isotope values (correlated carbonate $\delta^{13}C$ and $\delta^{18}O$ and $\delta^{13}C$ values of $< –5‰$ [Retallack, 2012]) are simply not relevant to interpretation of the depositional setting of the Ediacara Member and cannot be used as diagnostic paleoenvironmental indicators.

2.4. Sedimentological indications of exposure and paleosol development

Previous interpretations of fossiliferous horizons of the Ediacara Member have relied in large part upon petrographic and macroscopic features described as diagnostic of a subaerial, paleosol origin, such as "shrinkage cracks" (Retallack, 2012, figs. 8B, 9A–B), "gypsum rosettes" or pseudomorphs (Retallack, 2012, figs. 8E, 9G–H), "filaments" (Retallack, 2012, figs. 8C, 9A, D–F) and "branching tubular structures" (Retallack, 2013, figs. 2C–G; 2012, fig. 9B–C). The first two of these (shrinkage cracks and gypsum rosettes) would indeed, if present, provide compelling evidence of at least ephemeral evaporative conditions and thus an intertidal or otherwise marginal or terrestrial paleoenvironmental interpretation would not be unreasonable. However, we do not find recently published images (Retallack, 2012, fig. 8E, 9G–H) to provide convincing examples of either shrinkage (exposure) cracks or gypsum rosettes, nor have other attempts to find such features in the fossiliferous Ediacara Member, either prior to or following Retallack's studies, proved successful. The features identified by Retallack may simply be linked to late-stage fluid flow, an explanation wholly consistent with the evidence for alteration apparent in these successions. Further, even if gypsum pseudomorphs could be identified, the current lack of gypsum itself would indicate that late-stage fluid flow (responsible for removal of the anhydrite) has occurred and that, therefore, a diagenetic origin for some or all of these features certainly cannot be ruled out. The evidence previously presented for gypsum in these beds does not meet the standard of acceptability established by other workers' recent efforts to make a case for Precambrian gypsum, such as mold morphology and spatial distribution, fluid-inclusion composition and association with other, unequivocal exposure features (e.g. Schröder et al., 2008). Given the weight placed upon the extent of gypsum development as a metric for the presence and age of paleosols (e.g. see comparison with *Dickinsonia* size; Retallack, 2013, fig. 3) in the Ediacara Member, the correct identification of these features is paramount. The only strong candidates for sand pseudomorphs after gypsum previously illustrated for the Rawnsley Quartzite occur in the underlying Chace Quartzite Member (e.g. Facies Association A of Gehling, 2000, fig. 7F), which has been interpreted as supratidal. Yet recent efforts directed at the detection of Ediacara paleosols have focused solely upon the Ediacara Member rather than the more parsimonious candidate of the Chace Quartzite Member.

Likewise, "filaments" or "branching tubular structures" do not provide convincing evidence of exposure and syndepositional pedogenesis, nor do recent attempts to identify these features in fossiliferous facies of the Ediacara Member stand up under scrutiny. For instance, we are unable to recognize anything matching the description of "branching tubular structures extend[ing] deep into the paleosols" (Retallack, 2013, p. 90, fig. 2C–G). On the contrary, figured "filaments" and "tubules" (Retallack, 2012, fig. 9) are just as, if not more, likely to be diagenetic or tectonic in origin (see, for instance, the highly variable orientations of the "drab filamentous structures" indicated in fig. 9D and the obviously cross-cutting calcite vein in fig. 9E of Retallack (2012)). Moreover, even if these putative "tubules" could be interpreted as primary (syndepositional) in origin (which seems unlikely from their morphology), penetrative tubular structures are certainly not confined to terrestrial plants or lichens. Marine algae also possess penetrative tubular structures (e.g. rhizomes) and a wide variety of fossils of probable algal affinity are known from the Ediacara Member (Xiao et al., 2013), as well as from other Ediacaran-aged successions, such as the Lantian and Miaohe Biotas of South China (Xiao et al., 2002; Yuan et al., 2011). The presence of tubular structures is therefore not a feature unique to terrestrial organisms.

A bimodal grain size distribution has also been recently mooted as diagnostic of a terrestrial origin for the Ediacara Member (Retallack, 2013). We counter that this is merely an issue of provenance, and that marine rocks are just as likely as terrestrial rocks to have multiple sediment supply sources or energy regimes. Therefore grain size distribution cannot be employed as a diagnostic paleoenvironmental indicator.

2.5. Sedimentological indicators of a subaqueous depositional environment

In contrast, a broad range of sedimentary structures and facies relationships can be employed as diagnostic indicators of deposition under subaqueous conditions and can, in concert, be used to reconstruct a marine paleoenvironment. For instance, laterally continuous bedding, compositionally and texturally mature sediments, the presence of sedimentological features indicative of storm current- or wave-mediated sediment transport or erosion and fossilized remnants of organisms found only in marine settings are indicative of deposition in shallow marine environments (e.g. Plint, 2010). These features are commonly observed in the fossiliferous successions of the Ediacara Member, which can be demarcated into four distinctive facies, repeated in up to five parasequences across the Adelaide Geosyncline (Gehling, 2000; Gehling and Droser, 2013). At the base of each parasequence, red-colored, iron-rich, silty sandstones with linguoid ripples ("Delta-Front Sandstone Facies") are common. Fossils are preserved in hyporelief on the bases and in full relief within these beds. These beds are interpreted to have been rapidly deposited below wave base in a delta-front environment following the sea-level rise that marks the base of the Ediacara Member. The beds figured by Retallack (2013, fig. 2B) from Brachina Gorge are of this facies. The iron-rich sediment of the Delta-Front Sandstone Facies is likely derived from Mesoproterozoic alluvial sediments on the Gawler Platform, west of the Flinders Ranges (e.g. Drexel et al., 1993), and thus the ruddy coloration of this facies can be more parsimoniously interpreted to reflect the provenance of these clastic sediments, rather than "synsedimentary ferruginization" or syndepositional pedogenesis. This facies is overlain by light-colored, wave-rippled, medium- to coarse-grained laterally continuous arenitic sandstone beds with abundant body and trace fossils and well-developed textured organic surfaces preserved on bed bases and tops ("Wave-Base Sandstone Facies"; Fig. 3A–C). These sandstones are characterized by a high degree of both compositional and textural maturity. Both oscillatory and combined-flow ripples (e.g. Fig. 3B–C) are also common in this facies. Although oscillatory ripples alone are not necessarily diagnostic of a marine origin, they are nearly universally considered to be wave-produced (e.g. Walker, 1986; Boggs, 2006; Plint, 2010) and thus are diagnostic of a subaqueous origin in a substantial volume of water. However, interpretations of a terrestrial depositional setting for the Ediacara Member specify paleosols—subaerial soils—and the analogs upon which these claims have drawn are, moreover, desert soils (Retallack, 2013), not a large inland lake capable of sustaining oscillatory and storm-mediated combined flow. Therefore, to assert that fossiliferous horizons characterized by symmetrical ripples represent subaerially exposed surfaces, subsequently desiccated and terrestrially colonized, without evidence of exposure, exceeds the limits of parsimony. The compelling suite of sedimentary structures characterizing strata of the Wave-Base Sandstone Facies makes a terrestrial paleoenvironmental interpretation unlikely and much more strongly supports reconstruction as a shallow marine paleoenvironment, spanning fair-weather to storm wave base. Also overlying the Delta-Front Sandstone Facies are fossiliferous massive lenticular sandstone bodies ("Mass-Flow Sandstone Facies") which, along with breccias of recemented sandstone clasts, comprise a deep submarine canyon infill succession. Fossils occurring in these lenticular massive sandstones were likely entrained in and transported by dense bottom currents carrying fluidized sand; these fossils are preserved three-dimensionally within beds rather than along bed junctions

and are commonly characterized by an unusual degree of biostratinomic deformation. Rich fossil assemblages are additionally preserved along the interfaces of fine-grained, planar-laminated sandstone beds comprising another canyon-infill facies, the "Sheet-Flow Sandstone Facies" (Fig. 3D). These strata are characterized by erosive, non-rippled bases with abundant, crisply preserved tool marks of cm-scale length and bedding plane surfaces characterized by poorly developed matground textures and are interpreted to record event bed deposition below storm wave base. An empirical and process sedimentology-driven interpretation of this stratigraphic succession leads, most parsimoniously and entirely independently of consideration of the paleontological evidence, to reconstruction of deposition under marine, subaqueous conditions.

2.6. Fossil assemblages of the Ediacara Member

Various Ediacara fossils (or putative fossils) have been invoked as evidence for a paleosol origin for the Ediacara Member (Retallack, 2012, 2013). Here we address evidence for the biogenicity, affinity, habitat and preservational setting of several of these fossils:

The structure *Pseudorhizostomites*, which occurs commonly along fossiliferous horizons of the Wave-Base Sandstone Facies of the Ediacara Member, consists of a central invagination and radiating convex subparallel lineations. *Pseudorhizostomites* has been previously interpreted as a broad range of structures, such as a rhizostomean medusa or gas-escape structure (e.g. Glaessner and Wade, 1966; Sprigg, 1949; cf. Tarhan et al., 2010). It is not unlikely that *Pseudorhizostomites*, as currently defined, encompasses features of multiple origins. It has recently been suggested that *Pseudorhizostomites* is not a body fossil at all, but rather an ice crystal mold or the rim of a frozen microbial mound (Retallack, 2013).

However, *Pseudorhizostomites* occurring in strata of the Ediacara Member at Nilpena shares marked morphological similarities, such as a circular to ovoid external margin and radiating to subparallel lineations, with *Aspidella* and other holdfast taphomorphs such as the biotic tool mark "mop" (Tarhan et al., 2010) (Fig. 5C–D), all of which are characterized by a morphological continuum. To interpret these *Pseudorhizostomites* to have an origin entirely different from the rest of this continuum is simply not parsimonious. *Pseudorhizostomites* is commonly characterized by slightly asymmetrical spatial distribution of its subparallel, radiating lineations that suggests current-mediated deformation of a biogenic structure. This alignment, which is consistent with the orientation of other associated fossils also characterized by internally consistent alignment (and occurring on the same beds), such as ripped-up stalks (Fig. 5B), toppled fronds, 'uprooted' holdfasts (Tarhan et al., 2010) and fluid-mediated deformation of *Dickinsonia* (Evans et al., in 2015) (Fig. 5E), is indicative of current-mediated deformation and thus a subaqueous depositional environment. Moreover, *Aspidella* taphomorphs are commonly associated with stalks (e.g. Tarhan et al., 2010; Tarhan et al., 2015), which are likewise characterized by current-mediated alignment. The presence of stalks, in addition to the distinctive morphology of *Aspidella* and the preservation of taphomorphs and 'transitional' forms characterized by a combination of discoidal holdfast, stalk and frond (Fig. 5A), unequivocally indicates that these holdfasts are body fossils of an organism that contained all three elements and lived subaqueously in an environment characterized by intermittent events of strong fluid flow.

Likewise, we contend that the Ediacara fossil *Coronacollina* is not, as has been recently asserted (Retallack, 2013) an ice crystal mold. Rather, as described by Clites et al. (2012), the distinct morphology of this
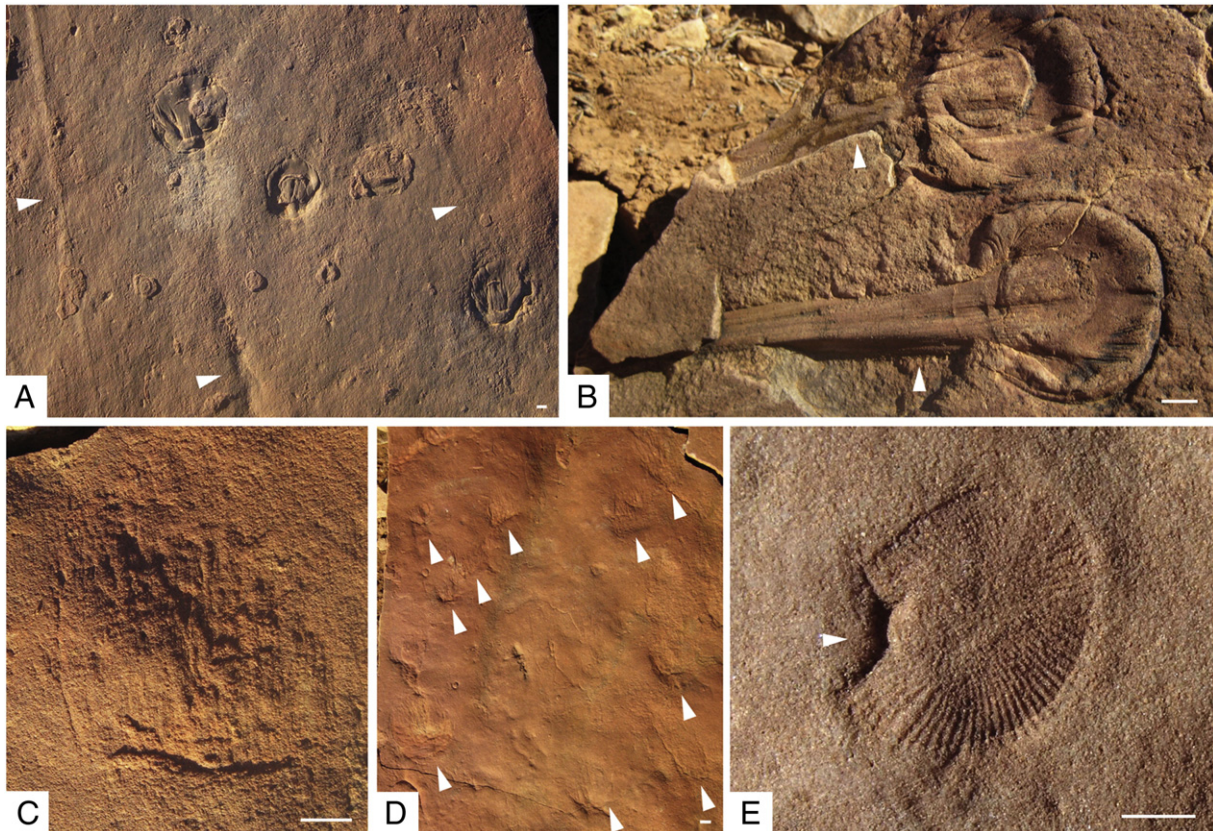

Fig. 5. Ediacara fossils exemplifying organism–current interactions. (A) Basal sandstone surface with multiple *Aspidella* holdfasts characterized by current-induced deformation, particularly creases and lineations produced by current-mediated tugging and removal of the organisms' stalks. Also note tool marks (white arrows) oriented parallel to *Aspidella* strain features and vestigial stalk fragments. Hyporelief. NRB-02. (B) Two *Aspidella* attached to three-dimensionally entrained, current-aligned stalks. Hyporelief. SAM P46289. (C) "Mop," the biogenic structure created by current-induced dragging and removal of the holdfast of a frondose organism from the microbially bound seafloor. Hyporelief. MM4-05. (D) Sandstone bed base characterized by dense assemblage of unidirectionally aligned (within 10°) mops (white arrows). (E) *Dickinsonia* characterized by current-induced 'lifting' of the proximal or stossward side of the organism's external margin (see Evans et al., 2015). Hyporelief. MM3-10. Scale bars = 1 cm. Specimen SAM P46289 reposited in the South Australian Museum.

structure, observed patterns of disarticulation and its similarity to previously described Cambrian forms such as the demosponge *Choia* have led to its interpretation as an early example of a biomineralizing, multi-element organism and likely poriferan. Moreover, the size range and right-skewed size distribution of *Coronacollina* observed at Nilpena is consistent with that expected for the ontogenetic sequence of an in situ eukaryotic community colonized by means of continuous recruitment. All of these features are inconsistent with an abiogenic, ice crystal origin; the presence of *Coronacollina* can therefore not be used as an indicator for a terrestrial, subaerial paleoenvironment.

Similarly, fans of paired scratch marks or *Kimberichnus* (cf. Gehling et al., 2014) occurring in close spatial association with the Ediacara body fossil *Kimberella* (a putative stem-group mollusk or basal lophotrochozoan (Gehling et al., 2014)) have also been interpreted as ice crystal molds (Retallack, 2013). However, the consistent pairing and systematic association of these scratch marks with *Kimberella* much more strongly support a biological origin for these features (nor is it likely that formation of ice crystal arrays would be a species-specific phenomenon). Therefore, the presence of *Kimberichnus*, like that of *Coronacollina*, cannot be used as an indicator for a terrestrial, subaerial paleoenvironment.

Recent efforts to attribute a paleosol origin to the Ediacara Member have also interpreted Ediacara trace fossils as fungi, on the grounds that similar structures have previously been interpreted as slime molds. However, these putative slime molds (Rasmussen et al., 2002; Bengtson et al., 2007) have been heavily discredited on the basis of both morphology (e.g. tapering ridges, lack of uniform width) and taphonomy (positive-relief 'mucus' ridges preserved on the base of a bed, the improbability of preserving mucus at all) (e.g. Conway Morris, 2002; Droser et al., 2002; Budd and Jensen, 2003; Jensen, 2003; Jensen et al., 2006). Due to the lack of trace fossil-specific criteria, these structures should not be considered as appropriate evidence for a slime mold origin for genuine Ediacaran trace fossils such as *Helminthoidichnites*.

Many elements of the Ediacara Biota are known from other, globally-distributed Ediacaran deposits which have been independently demonstrated to be of marine origin. For instance, the Ediacaran macro-fossil record of South China includes several globally-known Ediacara taxa, such as the eight-armed *Eoandromeda*, cup-shaped *Nemiana*, frondose fossils, *Flabelophyton*- and *Gesinella*-like filamentous fossils, *Beltanelliformis* discoidal fossils and *Helminthoidichnites* trace fossils (Grotzinger et al., 2000; Narbonne, 2005; Zhu et al., 2008; Xiao et al., 2013). *Helminthoidichnites* is known not only from Chinese dolomites but also from fine-grained sandstones of northwestern Canada. It is therefore difficult to see how these fossils of distinct and strikingly disparate morphology, occurring worldwide in a broad range of facies, each of which has been independently interpreted to represent a marine paleoenvironment, could be reasonably interpreted to all fall under the category of slime-molds or lichens from a terrestrial paleoenvironment.

Further, arguments in favor of a lichen affinity for the Ediacara Biota (e.g. Retallack, 2013) have invoked the presence of lichen-like organisms in other Ediacaran-aged deposits (Yuan et al., 2005). However, the mere existence of non-metazoan eukaryotes, such as lichen-like organisms or protists (which of course are known from even older, Cryogenian-aged deposits [e.g. Bosak et al., 2011; Cohen et al., 2011]) is not evidence for a lack of Ediacaran metazoans—these life forms are not mutually exclusive. The mere contemporaneity of a group is insufficient grounds for paleobiological, let alone paleoenvironmental interpretation; paleoenvironmental assessment must be carried out on the basis of first-order empirical observations, interpreted in a sedimentological process-driven context. It has likewise been suggested that terrestrial organisms grow and diversify as substrates age (Retallack, 2013, p. 91). However, this relationship is certainly not unique to terrestrial communities; organismal size ranges and distributions, therefore, cannot be used to assess paleoenvironment. In fact, we would suggest that diversification with age is a key characteristic of any community, marine or terrestrial. A terrestrial affinity for a particular fossil needs

to be independently demonstrated according to morphological and sedimentological criteria specific to each fossil. Sweeping generalizations and analogies with either dubiofossils or modern structures from dissimilar environments (e.g. Retallack, 2013, fig. S2, Table S2) and of dissimilar life modes is neither a compelling nor a parsimonious approach.

2.7. Modern and ancient microbial substrates

Textured organic surfaces (TOS) are the fossilized remnants of organically (e.g. microbially) bound substrates and are characterized by distinctive and repeating morphological elements. "Old elephant skin" is but one of many TOS found on fossiliferous beds of the Ediacara Member (Gehling and Droser, 2009). Like Ediacara body fossil assemblages, the composition, density and relative abundance of TOS vary between beds. We therefore find it impossible to interpret TOS as anything but organic in origin and we interpret variability in TOS morphology, density and spatial distribution to reflect not only variability in facies but also variable composition of the mat-forming consortia (which likely included eukaryotes, as well as prokaryotes). Recently, it has been suggested that the Ediacara substrate was not associated with microbial mats because "aquatic microbial mats are laminated, and detachable from their mineral substrate as flakes, skeins and rollups, not seen in the Ediacara Member" and due to the lack of "laminar to domed (stromatolitic) increments" supposedly characteristic of microbial mats (Retallack, 2013, p. 90). However, this description grossly underestimates the diversity of marine microbial mats. The texture of both modern and ancient (e.g. Tarhan et al., 2010) microbial 'mats' runs the gamut of thick 'gunky' mats to biofilm and their behavior under fluid flow and stratigraphic expression can be expected to vary accordingly. Moreover, a microbial mat-bound interpretation of the Ediacara substrate does not preclude either a deep or diffuse presence of microbes. Although there are of course some modern microbial mats that are characterized by thick and gelatinous layers of microbial communities with a minor sediment component, there are also numerous described examples of sediment-rich, sandy mats characterized by a pervasive and deep microbial presence. These sediment-rich mats behave cohesively upon disturbance and occur in subaqueous marine environments. Certain intertidal to subtidal microbial mats growing on the Bahamian Platform, for instance, are commonly very sandy and will resist being ripped up by even hurricane-associated fluid flow (e.g. Reid et al., 1995). Nonetheless, mat chips and rip-ups—features which Retallack (2013) associates with microbial mats—do indeed occur in the incised valley-fill facies (e.g. Mass-Flow Sandstone Facies) at Nilpena. Lastly, we object to the idea that being "embedded in the surface layer" (Retallack, 2013, p. 90) precludes an organically bound interpretation of the Ediacara substrate and a marine interpretation of the Ediacara depositional environment and we find that a facile comparison to modern desert crusts (entirely dissimilar from the coastal and intermittently subaqueous soils invoked by Retallack (2013, fig. S2)) is insufficient to rule out an affinity to marine microbial mats. Not all marine mats are "tuft[ed]" or "dom[ed]" (Retallack, 2013, p. 90) and mats as a whole—siliciclastic or carbonate—far surpass the diversity encompassed in the term "stromatolite."

3. Discussion

The process of paleosol formation is essentially one of weathering and reworking and the South Australian surface, which has been tectonically stable, subaerially exposed and unglaciated since the Permian (e.g. Milnes et al., 1985; Bird and Chivas, 1988; Kohn et al., 2002; Anand, 2005; Pillans, 2007), no doubt contains well-developed paleosols. But we find no convincing evidence for the presence of synsedimentary (Ediacaran) paleosols within the fossiliferous Ediacara Member. On the contrary, there are strong sedimentological data indicating late-stage mobility of iron within the Ediacara Member, directly

conflicting with previous suggestions. Sedimentological features, facies relationships, regional paleogeography, and the morphology, orientation and biostratinomy of fossil assemblages all suggest that the fossiliferous Ediacara Member was deposited in shallow marine, wave- and storm-influenced environments. A rigorous and process-driven sedimentological assessment of the facies relationships of these assemblages provides unique insight into not only the habitats of these seminal complex communities, but also the physical, chemical and biological conditions that facilitated their preservation in the fossil record.

Moreover, previous arguments for a terrestrial origin for the fossiliferous Ediacara Member have relied largely on non-parsimonious interpretations of Ediacara sedimentology and paleontology, employing non-diagnostic or invalid proxies for paleosol formation and 'synsedimentary ferruginization.' However, multiple questionable lines of evidence to not constitute a convincing argument for a terrestrial origin of the fossiliferous Ediacara Member.

It has long been recognized that color is not an appropriate proxy for paleoenvironmental reconstruction; red coloration reflects the presence of ferric iron, but ferric iron does not necessitate a terrestrial depositional setting, nor does the presence of modern ferric iron, particularly where variations in color do not follow bedforms and are clearly related to late-stage fluid flow, necessarily reflect syndepositional conditions. Carbonate nodules are, likewise, not diagnostic of a particular depositional environment. As has been amply demonstrated in the last four decades of geochemical literature, neither the presence of nodules nor intra-nodule depleted oxygen or carbon isotope signatures uniquely reflect a terrestrial origin. The fossiliferous Ediacara Member lacks any evidence of contemporaneous exposure; features such as mudcracks and syndepositional evaporites are entirely absent. Such features have been observed in the unfossiliferous Chace Quartzite Member of the Rawnsley Quartzite and in the underlying Bonney Sandstone. However, surprisingly, none of the recent efforts to detect paleosols in the Ediacaran of South Australia have been directed toward either of these units, but have instead focused solely on the fossiliferous Ediacara Member. However, all fossiliferous facies of the Ediacara Member are of demonstrably marine origin, characterized by laterally continuous beds of mature sandstone, with features ranging from oscillatory and combined-flow ripples to planar lamination and tool marks. Fossils in these assemblages are commonly characterized by current alignment or current-mediated deformation, as well as size distributions and reproductive strategies characteristic of marine invertebrate populations today. The Ediacara substrate was characterized by a high diversity of organically-mediated textures, reflecting the presence of a rich and complex consortia of micro- and macro-organisms, likely ranging from archaeal and bacterial to eukaryotic. The breadth of complex physiologies, ecological interactions and facies relationships represented in the Ediacara Member indicate that eukaryotic life had, by the late Ediacaran Period, established a strong foothold in the marine biosphere.

4. Conclusions

We discuss a range of proxies that have been or can be used for paleoenvironmental assessment of the Ediacara Member and assess their validity and usefulness.

1. Color is neither a useful nor a diagnostic property; color is as likely to reflect the late-stage diagenetic or alteration history of a body of rock as it is to reflect synsedimentary processes. Moreover, great care must be taken to ascertain whether ferric oxides are surficial or penetrative, and whether they adhere to bedform relationships. Ferric oxides in the Ediacara Member consist largely of surficial staining which is not bed-parallel and commonly includes classic late-stage features such as Liesegang banding, intra-bed patchiness and sharp gradations in color along bedding plane surfaces.
2. Neither carbonate nodules nor their oxygen and carbon isotopic signatures can be construed as uniquely terrestrial; nodules have long been

recognized from marine successions and may form at any stage in the burial history of a succession.

3. The fossiliferous Ediacara Member is entirely lacking in exposure features. Neither mudcracks nor synsedimentary gypsum have ever been observed by us in the fossiliferous facies of this unit. On the contrary, sedimentological features and facies relationships all suggest a subaqueous, marine origin, with a transect spanning from within the zone of fair-weather wave oscillation to distal storm wave base.
4. Fossils of the Ediacara Member are demonstrably organic in nature and are, across a wide range of taxa, morphologies and facies, commonly characterized by features indicating interaction with subaqueous currents.
5. The Ediacara Member is characterized by not only rich and heterogeneous assemblages of body fossils and trace fossils, but also a comparable richness of TOS fabrics, which indicates that the Ediacaran Period was unique in the diversity and distribution of 'matground' communities, which served as the foundation for a range of complex ecological interactions and physiological innovations.
6. Multiple lines of evidence have been put forward to suggest that the Ediacara Member was deposited in a terrestrial setting. Some of the sedimentological and geochemical features of the Ediacara Member may not, individually, be inconsistent with a terrestrial environment. However, and importantly, none of these features are diagnostic of a terrestrial environment and the suite of features characteristic of the Ediacara Member can be interpreted far more parsimoniously as marine in origin. Myriad lines of weak and inconclusive evidence do not constitute a compelling argument in favor of a terrestrial paleoenvironment. The fossiliferous Ediacara Member is most parsimoniously interpreted as a succession of sedimentary packages deposited in a shallow marine setting. There is no evidence that the Ediacara Biota, as preserved in the geologic record of South Australia or elsewhere, represents an experimental terrestrial ecosystem.

Acknowledgments

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