LETTER

Ediacaran life on land

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Ediacaran (635–542 million years ago) fossils have been regarded as early animal ancestors of the Cambrian evolutionary explosion of marine invertebrate phyla[1], as giant marine protists[2] and as lichenized fungi[3]. Recent documentation of palaeosols in the Ediacara Member of the Rawnsley Quartzite of South Australia[4] confirms past interpretations of lagoonal–aeolian deposition based on synsedimentary ferruginization and loessic texture[5,6]. Further evidence for palaeosols comes from non-marine facies, dilation cracks, soil nodules, sand crystals, stable isotopic data and mass balance geochemistry[4]. Here I show that the uppermost surfaces of the palaeosols have a variety of fossils in growth position, including *Charniodiscus*, *Dickinsonia*, *Hallidaya*, *Parvancorina*, *Phyllozoon*, *Praecambridium*, *Rugoconites*, *Tribrachidium* and 'old-elephant skin' (ichnogenus *Rivularites*[7]). These fossils were preserved as ferruginous impressions, like plant fossils[8], and biological soil crusts[9,10] of Phanerozoic eon sandy palaeosols. Sand crystals after gypsum[11] and nodules of carbonate[12] are shallow within the palaeosols[4], even after correcting for burial compaction[13]. Periglacial involutions and modest geochemical differentiation of the palaeosols are evidence of a dry, cold temperate Ediacaran palaeoclimate in South Australia[4]. This new interpretation of some Ediacaran fossils as large sessile organisms of cool, dry soils, is compatible with observations that Ediacaran fossils were similar in appearance and preservation to lichens and other microbial colonies of biological soil crusts[3], rather than marine animals[1], or protists[2].

Newly documented palaeosols in the Ediacara Member of the Rawnsley Quartzite in South Australia[4] now call for a re-evaluation of its famous fossils, widely considered evolutionary predecessors of the Cambrian explosion of marine animal phyla[1]. Ediacaran red beds of South Australia (Figs 1 and 2) were initially considered non-marine by Douglas Mawson and Ralph Segnit[5]. When Mawson's student Reginald Sprigg discovered and interpreted South Australian Ediacaran fossils as marine jellyfish[14], this palaeoenvironmental contradiction was resolved by a compromise interpretation of jellyfish thrown up onto tidal flats by storms[15]. Ediacaran fossils are known worldwide in a variety of sedimentary facies[16], generally interpreted as shallow to deep marine, following Sprigg's[14] comparison with marine animals[1], although such comparisons now seem increasingly doubtful. Most Ediacaran fossils have no clear relationship with modern animals[2,3,16,17]. Putative Neoproterozoic 'embryos' were more likely to have been protists[18]. Putative permineralized metazoans may instead have been crystal-lined vughs[19], and other permineralized Ediacaran fossils were red algae or glomeromycotan lichens[20]. Precambrian shallow trails may have been made by slime moulds in their slug aggregation phase rather than worms[21]. There have also been suggestions that Ediacaran fossils were giant protists, such as xenophyophores[2], or fungi, such as lichens[3].

Palaeosols in the Ediacara Member have been overlooked until now, because they are less strongly developed than palaeosols at Precambrian unconformities or formed under forests of the Devonian period and later[4]. In addition to obvious soil structures (platy peds) and horizons (A-Bk and A-By), bedding disruption on mainly microscopic scales contributes to the massive appearance of palaeosols compared with sedimentary rocks in the field (Fig. 2b–e). One bed (Warrutu palaeosol of Fig. 2b) has four distinct episodes of soft sediment deformation followed by successive weathering and bedding disruption of previous episodes, comparable with successive periglacial soil involutions, rather than seismic or load deformation[4]. Further evidence for Ediacaran palaeosols, detailed elsewhere[4] includes (1) geochemical mass-balance negative strain and cation mass transfer; (2) loessic grain-size distribution and texture; (3) unusually light carbon and oxygen isotopic compositions that show linear covariance; and (4) sand crystals of gypsum and micritic replacive nodules with a consistent depth from the tops of beds. The 47 different stratigraphic levels showing pedogenic features in Brachina Gorge (Fig. 1) are repetitions of five distinct types of palaeosol named as pedotypes from the Adnamatna indigenous language (see Supplementary Information, Supplementary Fig. 2 and Supplementary Tables 1 and 2).

The red colour and weathering of rocks in the Flinders Ranges have been regarded as products of deep weathering from the Cretaceous period or later[22], but this view is falsified by several observations. Red beds of the Ediacara Member have been found beneath grey shales and limestones in drill cores in the Ediacara hills, where the cores have the same unusual and distinctive carbonate carbon isotopic composition and major element composition as the outcrops in Brachina Gorge[4]. Grey sandstone palaeochannels of the Ediacara Member include red clasts redeposited from the Ediacara Member and Bonney Sandstone, as well as grey calcareous clasts from the Wonoka Formation: all should be red if they were weathered downwards from the current land surface. A variety of clay crystallinity indices, X-ray diffraction data and microprobe analyses demonstrate that the Ediacara Member in outcrop and core is illite-chlorite that has been heated to low within the greenschist metamorphic facies[4] (see Supplementary Information, Supplementary Figs 3–6 and Supplementary Table 4). Furthermore, Ediacara Member sandstones contain abundant feldspar, and red siltstones include carbonate nodules. By contrast, deep weathering profiles contain no feldspar nor carbonate, and have kaolinite clays and a chemical composition strongly depleted in alkali and alkaline earth elements[4]. The red colour and degree of weathering do not distinguish palaeosols from sediments, because both can be acquired from soils in source terrains, but the relative timing of reddening and weathering is crucial to a terrestrial–aeolian interpretation[5].

Palaeosols and fossils of the Ediacara Member are distinguished by a surface texture called old-elephant skin, which is best preserved under covering sandstone beds[7]. *Rivularites repertus* is a validly named ichnospecies for comparable cracked and pustulose surfaces[7]. What makes it look old is healed cracks, irregular fine ridges (cracks in cover sandstone), and pustulose relief of intergrown radial growth centres (Fig. 2a). These distinctive cracked and pustulose surfaces have a variety of features that are more like the biological soil crusts of desert and tundra[9,10] than the parallel-wrinkled, and undulose hydrated microbial mats of intertidal flats and shallow seas[7]. Biological soil crusts and their soils have vertically oriented organisms intimately admixed with minerals of the soil, whereas aquatic microbial mats are laminated, and detachable from their mineral substrate as flakes, skeins and rollups, not seen in the Ediacara Member. Soil crusts have irregular relief, healed desiccation cracks and pressure ridges even in clay-poor sandstones, whereas microbial mats have flexuous, striated domes and tufts, again not seen in the Ediacara Member. Soil crusts are

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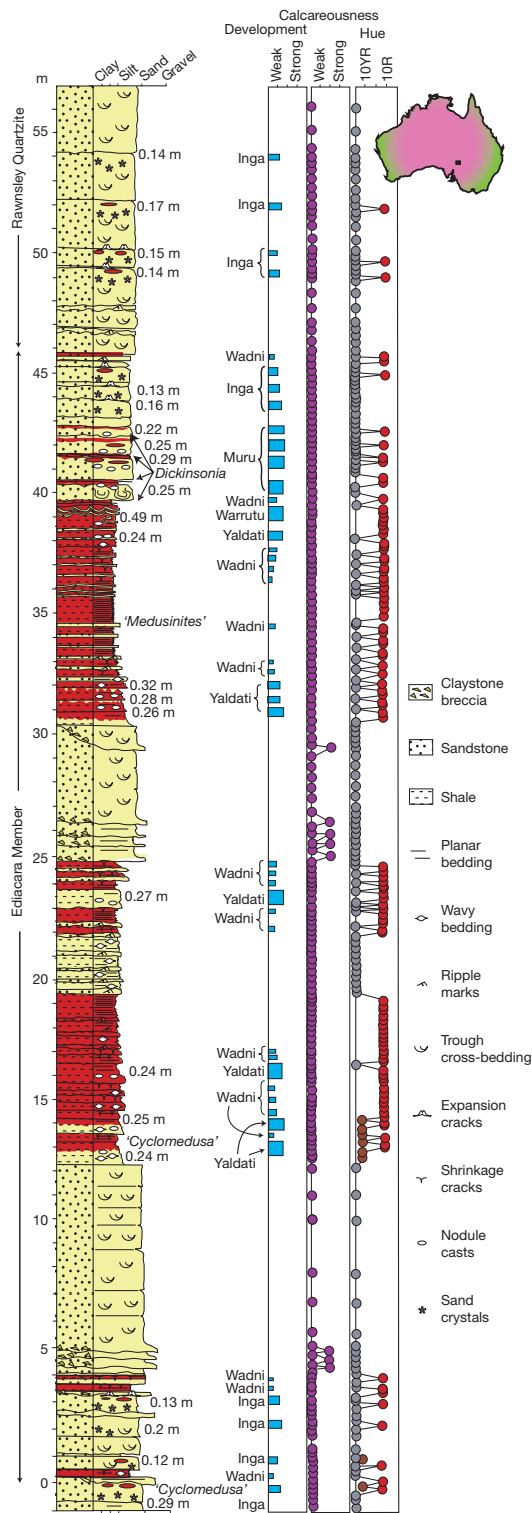
Figure 1 | Geological section of upper Ediacara Member in Brachina Gorge, South Australia. The interpreted palaeosol position and development (height and width of black boxes, respectively[4]) are shown. Calcareousness assessed in field by degree of reaction with 10% stock HCl. Hues such as 10YR and 10R are from a Munsell chart. This was the entire Ediacara Member as originally defined[6] in the Brachina Gorge (31.34422° S, 138.55763° E).

the upper part of deeper soil profiles with downward variation in oxidation, clay abundance and replacive nodular subsurface horizons like palaeosols of the Ediacara Member, whereas microbial mats form caps to unweathered, chemically reduced sedimentary layers. Soil crusts develop increasingly differentiated soil profiles through time,

whereas microbial mats build upwards in laminar to domed (stromatolitic) increments. Sandy palaeosols with impressions of lichen-like fossils are also known from Ordovician[9] and Cretaceous palaeosols[10]. Comparable preservation of vascular land plants is well known in red sandy palaeosols of Cretaceous age[8].

Ediacaran fossils were preserved as impressions in old-elephant skin sandstones overlying four of the five different kinds of palaeosol at ten different horizons in four classic localities (see Supplementary Information and Supplementary Table 3). The best place to see Ediacaran fossils in place above a palaeosol is the overhang at the 39.7 m level in Brachina Gorge (Fig. 2b), where there are still good specimens of *Dickinsonia costata* and *Pseudorhizostomites howchini*. The body fossils were firmly attached or embedded within these soil surfaces in life, as revealed by growth series, lack of overlapping specimens, and thickening of adjacent specimens comparable with competitive reaction[3,22]. Some taxa such as *Phyllozoon hanseni* and *Aulozoon* sp. are embedded within the surface layer, like window lichens and rhizines in desert crusts[3]. In petrographic thin sections, branching tubular structures extend deep into the palaeosols (Fig. 2c–g), like cyanobacterial ropes, fungal hyphae and lichen rhizines of desert crust soils today[7]. Petrographic thin sections of the lower half of impressions of *Dickinsonia* fossils show comparable bedding disruption by irregular tubular features (Fig. 2c, d): the more common upper impression fossils show only bedded sandstone overlying the fossil (Fig. 2e). Comparable bifacial fossil features, with smooth and finished upper surfaces but ragged lower surfaces, were also found in surface horizons of the palaeosols (Fig. 2e–g). Which specific Ediacaran fossils are represented by these thin sections is uncertain, because Ediacaran taxa have been defined by shape, not appearance in thin section. These images of complex chambered structures with basal tubules (Fig. 2c–g) are preliminary indications of their appearance in thin section prepared for a detailed study in progress. Observed cross-sections of Ediacaran fossils in petrographic thin sections are comparable in preservational style with plants and lichens in Phanerozoic palaeosols[8–10].

Body fossils so far documented on the palaeosols include '*Aulozoon*' sp. indet., *Charniodiscus arboreus*, '*Cyclomedusa davidi*', *Dickinsonia costata*, *D. elongata*, *D. rex.*, *Hallidaya brueri*, cf. '*Kimberella*' sp. indet., '*Medusinites asteroides*', *Parvancorina minchami*, *Phyllozoon hanseni*, *Praecambridium sigillum*, *Rugoconites enigmaticus*, *Spriggina floundersi* and *Tribrachidium heraldicum*. Trace fossils found in the palaeosols include *Archaeonassa* sp. indet., *Pseudorhizostomites howchini*, cf. '*Radulichnus*' sp. indet. and *Rivularites repertus* (see Supplementary Information and Supplementary Table 3). Some palaeosols (Muru and Wadni pedotypes) have a diverse fossil assemblage dominated by *Dickinsonia*, whereas others (Yaldati and Inga) have a low-diversity assemblage mainly of discoid fossils (variously attributed to microbial colonies, medusoids or holdfasts, and taxa such as *Medusinites* and *Cyclomedusa*[1]). One palaeosol with deformation interpreted as periglacial involutions[4] (Warrutu pedotype) yielded no fossil specimens in outcrops, but may have Ediacaran fossils in thin sections (Fig. 2f, g). These differences in diversity may be evidence that Ediacaran organisms preferred unfrozen, low salinity soils, rich in nutrients, like most terrestrial organisms.

Not only fossil diversity, but fossil size may have increased with palaeosol development. The relationship between gypsum abundance (G in area (%)) and geological age (A in kyr) in the Sinai and Negev Deserts of Israel[23,24] is given by the following equation:

$$A = 3.987G + 5.774 \qquad (1)$$

This relationship ($R^2 = 0.95$) has the standard error ± 15 kyr. The largest *Dickinsonia* (32 cm long, *D. rex*[12]) from the main collecting gully in the Ediacara hills came from a Muru palaeosol with 10% gypsum, and using equation (1), was 53.6 ± 15 kyr in the making. Long-term growth of this *D. rex* (0.006 ± 0.002 mm yr^{-1}) would have been more like modern lichens (*Rhizocarpon geographicum*) in the Brooks Range
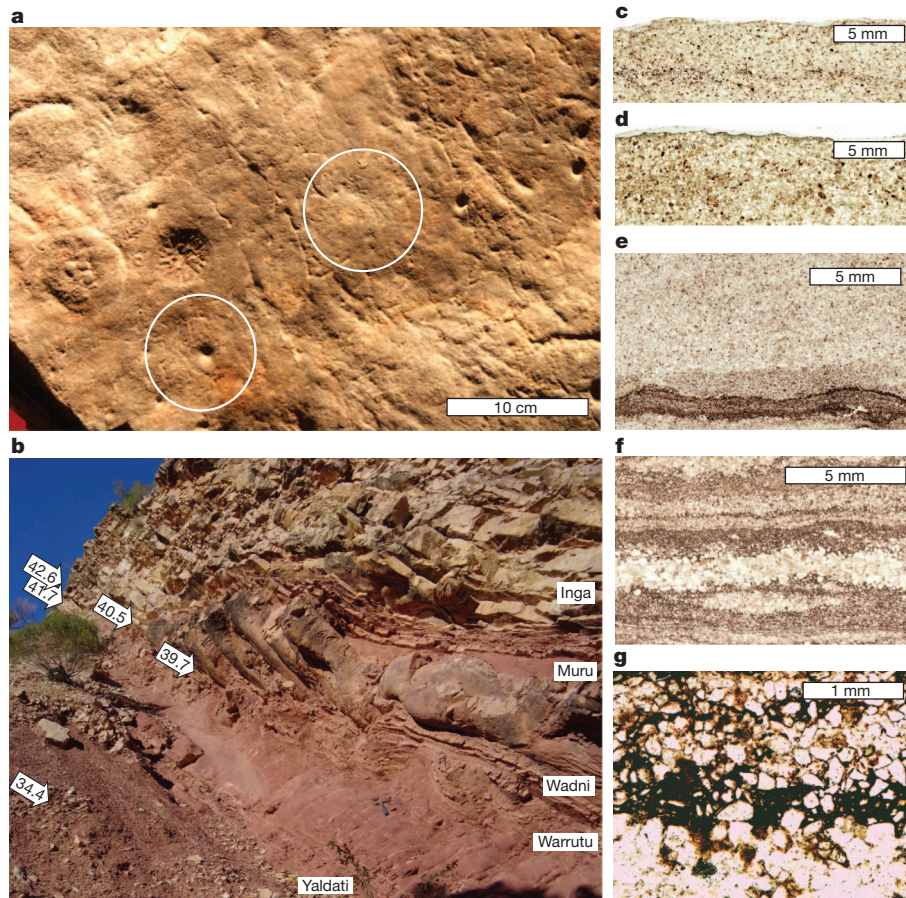
Figure 2 | Palaeosols of the Ediacara Member of the Rawnsley Quartzite, South Australia. a, *Rivularites repertus* (old-elephant skin) showing sutured radial growth, crack fills and ridge impressions, effaced discoid fossils (white circles) and fossil impressions (*Hallidaya brueri* in positive relief to left, and *Rugoconites enigmaticus* in negative relief to right), on sole of sandstone slab from Crisp Gorge (31.176572° S, 138.328533° E). **b**, Palaeosols and fossil levels in the Brachina Gorge (31.34422° S, 138.55763° E). **c, d**, Vertical petrographic thin sections of the lower part of *D. elongata* (**c**) and *D. costata* (**d**) showing bedding disruption and tubular features, from Muru palaeosol in the Ediacara hills (**c**) and unknown palaeosol at the Hookapunna well (**d**). **e–g**, Unidentified dorsoventral Ediacaran fossils in thin sections showing overlying cross-bedded sandstone (**e**) and basal irregular tubular structures (**e–g**). The fossiliferous surface in **a** is part of a large slab on display in the South Australian Museum, Adelaide. The hammer for scale in **b** has a length of 25 cm. Specimen numbers in the Condon Collection, Museum of Natural and Cultural History, University of Oregon are F112999 from Muru palaeosol in the Ediacara hills (**c**), F115736 from unknown palaeosol near the Hookapunna well (**d**), R3218 from Muru palaeosol in the Brachina Gorge (**e**), and both R3223 (**f**) and R3222 (**g**) are from the Warrutu palaeosol in the Brachina Gorge. All thin sections were cut vertical to regional bedding.

of northern Alaska (0.04 mm yr^{-1}) than lichens in southern Alaska[25] (0.1 mm yr^{-1}) or southern Norway[26] (0.5–0.7 mm yr^{-1}). Correlation between the largest *Dickinsonia* found within a collection and gypsum enrichment in the palaeosol of that collection is evidence for slow non-linear growth rates of *Dickinsonia* (Fig. 3, Supplementary Information and Supplementary Table 3). The Ediacara hills has yielded one of the most diverse assemblages known, and Ediacaran organisms may have diversified as well as grown with soil age, comparable with modern terrestrial communities.

Indications of palaeoclimate come from comparison of palaeosols in the Ediacara Member with modern soils. The closest modern analogue to Ediacaran gypsic palaeosols seems to be soilscapes on the coastal plain of the Caspian Sea near Atyrau, Kazakhstan (mean annual temperature 8 °C, mean annual precipitation 160 mm: map unit Zo16-3a of Orthic Solonchak, with associated Takyric and Gleyic Solonchaks[27]). Calcic palaeosols are found nearby in the Emba River floodplain (map units Xl 16-1ab and Jc 53-2c). Periglacial involutions in one palaeosol[4] support other evidence from dropstones for cold temperate palaeoclimate in the coeval Billy Springs Formation of the far northern Flinders Ranges[28]. Other indications of cool and dry palaeoclimate from climofunctions for modern soils are outlined in the Supplementary Information, Supplementary Fig. 7 and Supplementary Tables 5 and 6. The zone of best preservation of large Ediacaran fossils in the Flinders Ranges is thus near the gypsic–calcic soil ecotone, an important biotic boundary in modern temperate deserts, such as the Atacama[29] and Negev[23] Deserts.

Discovery of some Ediacaran fossils in the surface horizons of palaeosols does not mean that all Ediacaran fossils everywhere were

$$y = 4.17\ln(x) - 4.5$$
$$R^2 = 0.78$$
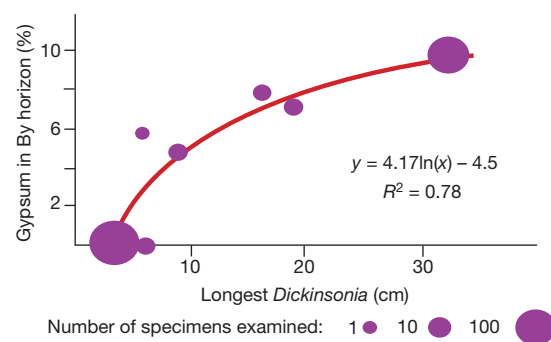
Figure 3 | Maximum length of *Dickinsonia* fossils related to area (%) of gypsum in same palaeosol, as a proxy for soil development. Measurements of the longest specimen from the largest collections are the most reliable (see Supplementary Information for data).

terrestrial. Intertidal to shallow marine facies recognized in the Ediacara Member[4], have so far proven unfossiliferous, but *Palaeopascichnus* is known from both old-elephant skin surfaces of the Ediacara Member interpreted here as terrestrial, as well as in pyritic black shales of the Wonoka Formation interpreted as marine[22]. Multisegmented fossils from palaeosols of the Ediacara Member such as *Dickinsonia*, *Charnia*, *Praecambridium* and *Spriggina* are more likely to have been lichens or other microbial consortia[3] than marine invertebrates[1] or giant protists[2]. Discoid Ediacaran fossils such as *Cyclomedusa*, *Medusinites* and *Rugoso-conites* would not be jellyfish in such dry soils, but could have been microbial colonies[30]. Small fossils such as *Parvancorina* or *Tribrachidium* could not have been pre-trilobites or proto-seat-stars[1], respectively, if they lived on land, but may have been fungal-fruiting bodies[3]. Trace fossils such as *Archaeonassa* could have been created by metazoan slugs or worms after rainstorms on land, but terrestrial habitats also open the possibility that these trails were created by slug-aggregating phases of slime moulds[21]. 'Radulichnus' impressions from the Ediacara Member are too straight and sharp to be molluscan radular scratches[2], and in cool temperate soils may instead have been casts of needle ice. *Pseudorhizostomites* has been considered a gas-escape structure in a marine setting[16], but as a soil-surface feature it is most like a flanged pedestal of a biological soil crust[7]. These surprising alternative terrestrial hypotheses for habitats and affinities of these enigmatic fossils arise largely from recognition of palaeosols, and their interpretation by comparison with modern soils and soil processes. These unconventional ideas and comparisons remain to be tested for different kinds of Ediacaran fossil, and in sequences and assemblages of Ediacaran fossils beyond South Australia.

METHODS SUMMARY

The main contribution of this Letter is to document the geographic and stratigraphic occurrence of Ediacaran fossils in palaeosols described in detail elsewhere[4], as well as new observations of Ediacaran fossils in petrographic thin sections. Further analytical data on these palaeosols are provided in the Supplementary Information and Supplementary Tables 4–6, and interpretation of their palaeoenvironmental setting is in Supplementary Tables 1, 2 and 7–9 and Supplementary Figs 2 and 7.

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