Precambrian life on land

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ABSTRACT

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Although Precambrian landscapes have been regarded as barren as the surface of Mars, increasingly close inspection of fossil soils (palaeosols) is revealing a variety of fossils, comparable with those already documented in Cambrian to Ordovician (542–444 Ma) palaeosols. The biggest surprise was that some Ediacaran (550 Ma) fossils of South Australia grew in soils. Different kinds of palaeosols can be used to define Ediacaran terrestrial communities in Australia (550 Ma) and Newfoundland (565 Ma). Simple discoids such as *Aspidella* dominate communities of intertidal sulfidic palaeosols, whereas quilted forms such as *Dickinsonia* dominate communities of well drained palaeosols. The discoids may be simple microbial colonies, but complex quilted fossils may be lichenized fungi. Complex quilted fossils appear in palaeosols during the Ediacaran along with large "acritarchs" (such as *Ceratosphaeridium*, and *Germinosphaera*) comparable with fungal chlamydospores and vesicles like those of Glomales (Glomeromycota). Discoid fossils and microbial filaments also are found in Palaeoproterozoic palaeosols, for example, in the 2100 Ma Stirling Range Quartzite of Western Australia. Complex Palaeoproterozoic (2200 Ma) fossils in South African palaeosols include *Diskagma*, comparable with the living endocyanotic *Geosiphon* (Archaeosporales, Glomeromycota). Archaean (2800 Ga) palaeosols of South Africa contain fossils such as *Thucomyces*, comparable with modern columnar biofilms. Even older terrestrial fossils may be represented by un–named spindle–like fossils from the 3000 Ma Farrel Quartzite and 3420 Ma Strelley Pool Formation of Western Australia. These spindle–like forms are comparable in morphology with modern soil actinobacteria, such as *Planomonospora*. Life on land may extend well back into geological history. Positive feedback for soil stabilization by formation of clay and organic matter, and the metered supply of water and nutrients in soils, make soils attractive sites for theories concerning the origin of life.

Key words—Fungus, Lichen, Microbial Colony, Palaeosol, Ediacaran.

भूमि पर कैंब्रियनपूर्व जीवन

जी.जे. रेटलैक

सारांश

यद्यपि कैंब्रियनपूर्व भू–दृश्य मंगल के पृष्ठ की भांति अनुर्वर माने गए हैं। कैंब्रियन से ऑर्डोविसियन (542–444 करोड़ वर्ष) पुरानिखातों में पहले से ही उन प्रलेखित के तुलनीय वृद्धित जीवाश्म मृदाओं (पुरानिखात) की सूक्ष्म जांच जीवाश्मों की विविधता उद्घाटित कर रही है। सबसे बड़े अचरज की बात थी कि दक्षिण आस्ट्रेलिया के कुछेक जीवाश्म इन मृदाओं में उगे। आस्ट्रेलिया (550 करोड़ वर्ष) और न्यूफाउंडलैंड (565 करोड़ वर्ष) में पुरानिखातों के विविध प्रकारों को इडियाकरन स्थलीय समुदायों को परिभाषित करने हेतु प्रयुक्त किया जा सकता है। *एस्पीडेल्ला* जैसे साधारण चक्रिक अंतःज्वारीय सलफाईटी पुरानिखातों के समुदायों को प्रभावित करते हैं, जबकि *डिकिनोसोनिया* जैसे गद्देदार प्ररूप सुवाहित पुरानिखातों के समुदायों को प्रभावित करते हैं। चक्रिक शायद साधारण सूक्ष्मजीव निवह हो, जबकि जटिल गद्देदार जीवाश्म लाइकेनीयुक्त कवक हो सकते हैं। कवक क्लैमिडो बीजाणुओं एवं ग्लोमेलों (ग्लोमेरोमायकोटा) के उन जलस्फोटिका सदृश के तुल्य विशाल "एक्रीटार्च" (जैसे कि *सेराटोस्फैरिडियम* एवं *जर्मिनोस्फैरा*) के साथ–साथ इडियाकरन के दौरान पुरानिखातों में जटिल गद्देदार जीवाश्म दिखते हैं। पुरा–प्राग्जीव पुरानिखातों में चक्रिक जीवाश्म और सूक्ष्म जीव खंडज भी मिले हैं, उदाहरणार्थ, 2100 करोड़ वर्षों में पश्चिमी आस्ट्रेलिया का स्टिर्लिंग रेन्ज क्वार्ट्ज़ाईट। दक्षिण अफ्रीकी पुरानिखातों में जटिल पुरा–प्राग्जीव (2200 करोड़ वर्ष) जीवाश्म जीवित एंडोसाएनोटिक *जिओसिफॉन* (आर्कियोस्फोरेल्स, ग्लोमेरोमायकोटा) के तुलनीय *डिस्कार्मा* सन्निहित हैं। दक्षिण अफ्रीका के आर्कियन (2800 Ga) पुरानिखात आधुनिक स्तंभीय जैवफिल्मों के तुल्य *तुकोमायसेस* जैसे जीवाश्म सन्निहित हैं। पश्चिमी आस्ट्रेलिया के 3000 करोड़ वर्ष फैरल क्वार्ट्ज़ाईट और 34 करोड़ 200 लाख वर्ष स्ट्रैल्ली पूल शैलसमूह से प्राप्त प्राचीनतर स्थलीय जीवाश्म भी नाम रहित तकुआ–सदृश जीवाश्मों से निरूपित हो सकते हैं। ये तकुआ–सदृश प्ररूप आकृतिविज्ञान में

प्लेनोमोनोस्पोरा जैसे आधुनिक मृदा प्रकाशजीवाणु के तुल्य हैं। पृथ्वी पर जीवन भू–वैज्ञानिक इतिहास के पूर्व तक हो सकता है। मृदा स्थिरीकरण हेतु सकारात्मक पुनर्भरण मिट्टी एवं कार्बनिक पदार्थ के गठन से तथा मृदा में जल एवं पोषक तत्वों की मापित पूर्ति जीवन के उद्भव संबंधी सिद्धांतों हेतु मृदाएं आकर्षक स्थल बनाती हैं।

सूचक शब्द—कवक, लाइकैन, सूक्ष्मजीवी निवह, पुरानिखात, ईडियाकरन।

INTRODUCTION

THERE is a pervasive bias in the teaching of geological history. According to many textbooks, before the Ordovician evolution of land plants the "landscape may have resembled that of barren Mars today" (Prothero & Dott, 2010; p. 255). A comparable insistence on no life on land before land plants has been urged in reviews of ancient river deposits (Davies & Gibling, 2010), to the controversial extent (Retallack, 2011a; Kennedy & Droser, 2012) of denying past accounts of Ordovician and Cambrian alluvial trace fossils and palaeosols (Davies *et al.*, 2010; Davies & Gibling, 2012), and overlooking evidence of Precambrian meandering channels (Button & Tyler, 1981; von der Borch *et al.*, 1989). Precambrian palaeobiology has focused on marine rocks (Knoll, 2003; Noffke & Awramik, 2013). "The basic strategy has remained unchanged since it was developed in the mid–1960's: look in black (carbon rich) cherts that are fine grained (unmetamorphosed) and associated with *Cryptozoon*–like stromatolites." (Schopf, 1999). Finally, there is the widely held philosophical view that life, "like Aphrodite, was born on the sea foam" (Bernal, 1961).
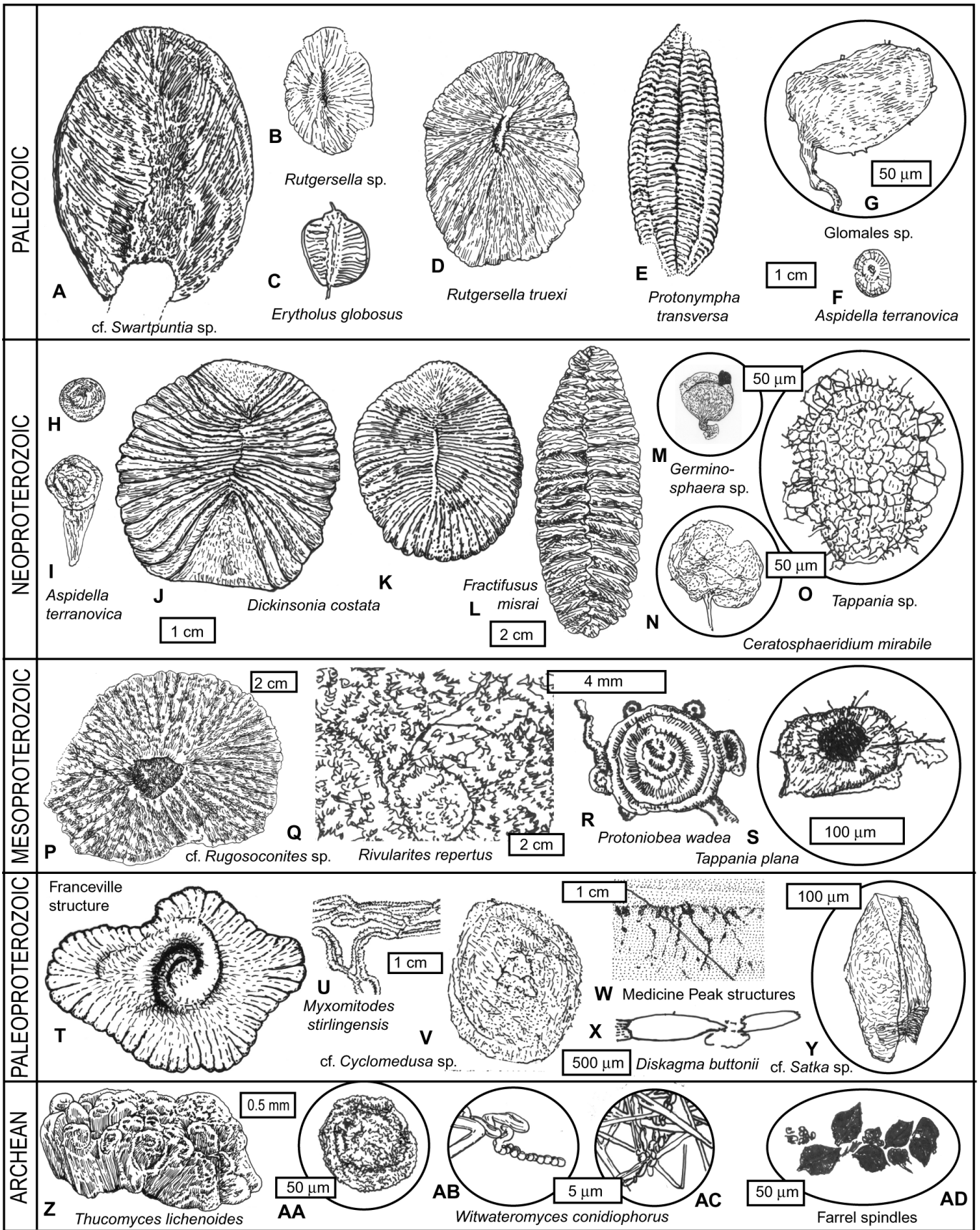
In contrast, studies of fossil soils are now providing evidence for life on land during both the Early Palaeozoic (Retallack, 2008, 2009, 2011a, b) and Precambrian (Mitchell & Sheldon, 2009, 2010; Driese *et al.*, 2011; Retallack *et al.*, 2013a). Although Precambrian palaeosols have been assumed lifeless for the purpose of using their chemical composition as a proxy for atmospheric conditions (Rye & Holland, 1998; Sheldon, 2006), there is now much evidence that Precambrian palaeosols were biologically active. One line of evidence is up–profile phosphorus depletion, which requires organic ligands (Neaman *et al.*, 2005; Dreise *et al.*, 2011; Retallack *et al.*, 2013a). Another line of evidence is isotopic compositions of oxygen and carbon in carbonate too light to have been marine (Retallack, 2012a). These and other geochemical proxies do not specify the kind of life, so this review emphasises fossils in palaeosols (Fig. 1), because fossils not only aid recognition of palaeosols, but also give indications of the kinds of life on land (Retallack, 2008, 2011b). Recognition of palaeosols has been a problem because early Palaeozoic and Precambrian palaeosols lack root traces of Silurian and later land plants, one of the most obvious and diagnostic features of palaeosols (Retallack, 1997). This leaves only the other two general criteria of soil horizons and soil structures (Retallack, 2012a, 2013a), which are unfamiliar to geologists, sedimentologists and palaeontologists. Without such field criteria, palaeosols are not recognised, nor sampled appropriately for geochemical confirmation (Retallack, 2012a, 2013a).

EDIACARAN *DICKINSONIA*

The deceptive near–symmetry of *Dickinsonia ovata* (Fig. 1D–E, 2A) has made it an icon for the diverse and enigmatic soft–bodied biota of the Ediacaran Period (542–635 Ma). At first *Dickinsonia* was considered a jellyfish (Sprigg, 1947), then different kinds of worm, beginning with turbellarian (Termier & Termier, 1968), then polychaete (Wade, 1972), and annelid (Conway Morris, 1979). *Dickinsonia* has also been considered a xenophyophore foraminifer (Zhuravlev, 1993), placozoan (Sperling & Vinther, 2010) and ctenophore (Zhang & Reitner, 2006). The near–symmetry, however, is not metamerically segmented, but alternating at the midline

Fig. 1—Summary diagram of Early Palaeozoic and Precambrian terrestrial fossils: A, Early Cambrian (540 Ma), Uratanna Formation, Mudlapena Gap, South Australia (Jensen *et al.*, 1998); B and F, Early Ordovician (483 Ma), Grindstone Range Sandstone, Wirrealpa, South Australia (Retallack, 2009); C, Middle Cambrian (509 Ma), Moodlatana Formation, Wirrealpa, South Australia (Retallack, 2011b); D, Early Silurian (440 Ma), Shawangunk Formation, Delaware Water Gap, Pennsylvania (Johnson & Fox, 1968); E, Middle Devonian (387 Ma), Moscow Formation, Summit, New York (Conway–Morris & Grazhdankin, 2006); G, Middle Ordovician (449 Ma), Guttenberg Formation, Wisconsin (Redecker *et al.*, 2000); H–I, Late Ediacaran (560 Ma), Fermeuse Formation, Ferryland, Newfoundland (Retallack, 2013b); J–K, Late Ediacaran (555 Ma), Zimny Gory Formation, Zimny Gory, Russia (Fedonkin, 1985); L, Middle Ediacaran (465 Ma), Mistaken Point Formation, Mistaken Point, Newfoundland (Gehling & Narbonne, 2007); M, Middle Ediacaran (610 Ma), ABC Range Quartzite, SCYW1a bore, South Australia (Grey, 2005); N, Late Ediacaran (570 Ma), Wilari Dolomite Member, Tanana Formation, Observatory Hill no. 1 well, northern South Australia (Grey, 2005); O, Cryogenian (820 ± 10 Ma) Wyniatt Formation, Victoria Island, Nunavut (Butterfield, 2005); P, Mesoproterozoic (1250 Ma), Pandwa Fall Sandstone, Gangau dam, India (Williams & Schmidt, 2003); Q, Mesoproterozoic (1480 Ma), Appekunny Argillite, Apekuni Falls, Montana (Retallack *et al.*, 2013b); R, Mesoproterozoic (1128 Ma), Mt John Shale Member, Osmond Range, Western Australia (McCall, 2006); S, Mesoproterozoic (1466 Ma), Roper Group, Crawford Point, Northern Territory (Javaux *et al.*, 2001); T, Palaeoproterozoic (2083 Ma), FB2 Formation, Franceville, Gabon (El Albani *et al.*, 2010); U–V, Palaeoproterozoic (2100 Ma) Stirling Range Formation, Barnett Peak, Western Australia (Bengtson *et al.*, 2007); W, Palaeoproterozoic (2000 Ma) Sugarloaf Quartzite, Medicine Peak, Wyoming (Kauffman & Steidtmann, 1981); X, Palaeoproterozoic (2200 Ma), Hekpoort Basalt, Waterval Onder, South Africa (Retallack *et al.*, 2013a); Y, Palaeoproterozoic (1800 Ma) Changzhougou Formation, Pangjiapu, China (Lamb *et al.*, 2009); Z–AC, Archaean (2800 Ma) Carbon Leader, Carletonville, South Africa (Hallbauer *et al.*, 1977); AD, Archaean (2970 Ma), Mt Grant, Western Australia (Sugitani *et al.*, 2007).

PALEOZOIC

A cf. *Swartpuntia* sp.

B *Rutgersella* sp.

C *Erytholus globosus*

D *Rutgersella truexi*

E *Protonympha transversa*

F *Aspidella terranovica*

G Glomales sp. 50 µm 1 cm

NEOPROTEROZOIC

H

I *Aspidella terranovica*

J *Dickinsonia costata* 1 cm

K

L *Fractifusus misrai* 2 cm

M *Germinosphaera* sp. 50 µm

N *Ceratosphaeridium mirabile* 50 µm

O *Tappania* sp. 50 µm

MESOPROTEROZOIC

P cf. *Rugosoconites* sp. 2 cm

Q *Rivularites repertus* 2 cm

R *Protoniobea wadea* 4 mm

S *Tappania plana* 100 µm

PALEOPROTEROZOIC

T Franceville structure

U *Myxomitodes stirlingensis* 1 cm

V cf. *Cyclomedusa* sp.

W Medicine Peak structures 1 cm

X *Diskagma buttonii* 500 µm

Y cf. *Satka* sp. 100 µm

ARCHEAN

Z *Thucomyces lichenoides* 0.5 mm

AA 50 µm

AB

AC *Witwateromyces conidiophorus* 5 µm

AD Farrel spindles 50 µm

(Fedonkin, 1985; Seilacher, 1989), and there is no sign of mouth, anus or coelom (Brasier & Antcliffe, 2008). The symmetry and construction of *Dickinsonia* is similar to that of the fractal–tubular fossil *Fractifusus* (Fig. 1L, 2C) from the Ediacaran (565 Ma) of Newfoundland (Gehling & Narbonne, 2007). Furthermore, *Dickinsonia's* degree of relief within the rock, despite substantial burial compaction, is incompatible with any of these soft bodied marine creatures, and is evidence of a rigid carapace with a biopolymer as compaction resistant as chitin (Retallack, 1994). My isotaphonomic study thus suggested surprising and controversial (Retallack, 2013b, c) affinities of *Dickinsonia* with fungi and lichens (Fig. 2B, D).

Other lines of evidence for fungal–lichen affinities of *Dickinsonia* include (1) unifacial structure, with finished and thick upper surface layer, but less distinct lower surface; (2) fractal tubular constructional and histological elements; (3) indeterminate isometric growth in width and length to maintain proportions; (4) indeterminate allometric growth in thickness to maintain ground–hugging form; (5) juvenile thallus unusually large and coarsely plicate compared with adult; (6) mature growth by radial addition of segments as well as diffuse marginal expansion; (7) marginal haloes comparable with hypothallial hyphae; (8) allelopathic avoidance of other individuals; (9) fairy ring arrangements of individuals; (10) decay series showing loss of relief but not of outline; (11) attached stout connecting rhizomorphs; and (12) limited marginal overturn and pull apart of thallus over expansion cracks indicating firm attachement to the silty substrate (Retallack, 2007a). A final line of evidence for lichen affinities came from discovery of *Dickinsonia* in life position within quartz–rich, oxidised, well drained gypsic and calcic palaeosols (Retallack, 2013d). *Dickinsonia* effaces primary sedimentary structures, such as ripple marks, by means of basal rhizine–like extensions down in to matrix, is always found on unusually complex microbially textured surfaces (Fig. 3A: "old elephant skin" or *Rivularites repertus*) characteristic of desert crusts (Fig. 3B), and shows growth coordinated with proxies for palaeosol development such as proportion of gypsum sand crystals (Retallack, 2012a, 2013d). Evidence for palaeosols beneath *Dickinsonia* and
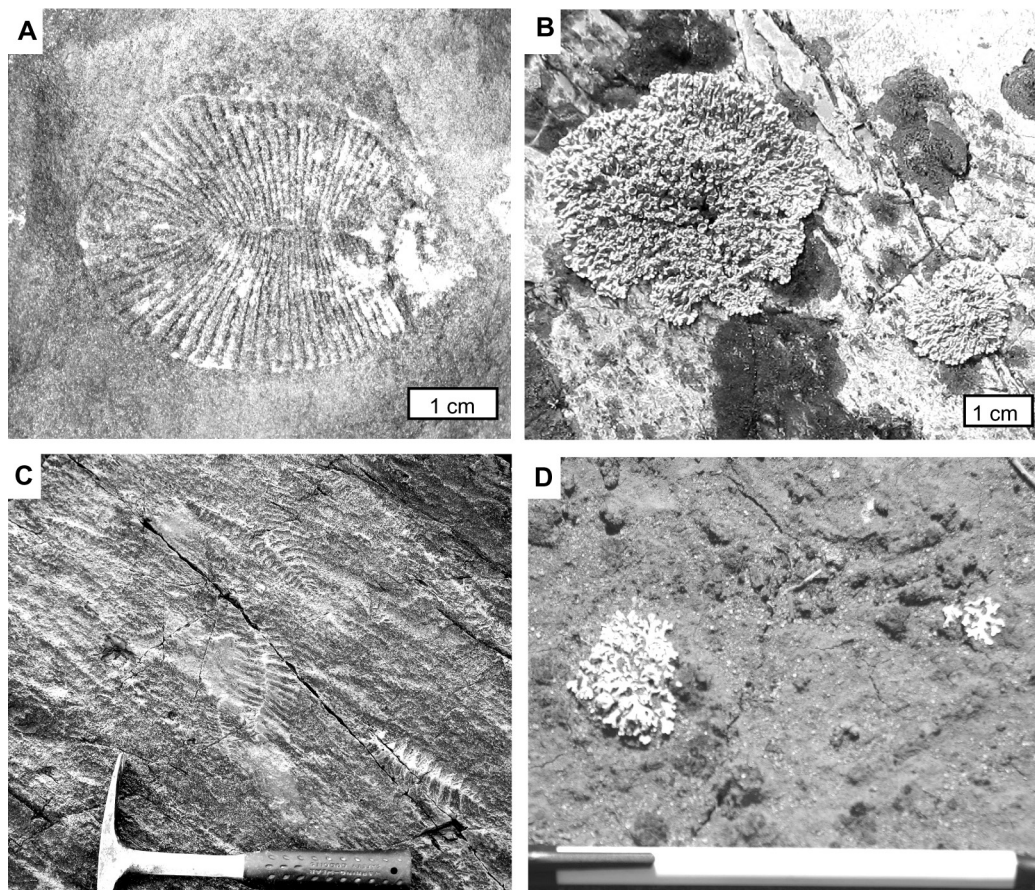

Fig. 2—Quilted Ediacaran fossils (A, C) and comparable living organisms (B, D); (A) *Dickinsonia ovata*, Ediacara Member (Ediacaran), Ediacara Hills, South Australia; (B) *Caloplaca verruculifera*, on rock, St Marys, Newfoundland; (C) *Fractifusus misrai*, Ediacaran Mistaken Point Formation, surface E at Mistaken Point, Newfoundland; (D) *Xanthoparmelia terrestris* on red soil at Back Creek, New South Wales, Australia. Specimen A is South Australian Museum 40299: others are field photographs.

other Ediacaran fossils includes unusually light carbon and oxygen isotopic composition in outcrop and drill core, geochemical mass balance showing loss of both volume and common cations, downward gradational destruction of bedding, drab–haloed filament traces (*Prasinema gracile*), soil crust pedestals, loess–like grain size and fabric, replacive (not displacive) sand crystals and nodules of calcite and gypsum at characteristic depth below bed tops, desiccation cracks, ice heave and melt structures, needle ice impressions, red redeposited soil clasts in grey fluvial sandstones, and red color of rocks with illitic–sericitic Ediacaran–style weathering and metamorphism rather than unmetamorphosed bauxitic and kaolinitic deep weathering (Retallack, 2012b, 2013d). The foregoing data suggest that *Dickinsonia* and associated Ediacaran (550 Ma) fossils in sandstones of South Australia lived in aridland soils (Fig. 4). Another round of work on Ediacaran fossil localities of Newfoundland is revealing humid climate coastal palaeosols there (Retallack, 2013a, 2014). Also under reexamination are early Palaeozoic localities for fossils

comparable with Ediacaran fossils (Johnson & Fox, 1968; Jensen *et al.*, 1998; Conway Morris & Grazhdankin, 2006).

South Australian and Newfoundland red beds may have been palaeosols with terrestrial organisms preserved in life position (Retallack, 2013a, d, 2014), and can be contrasted with marine grey shales and stromatolitic limestones, such as those of the Ediacaran (560 Ma) Wonoka Formation of South Australia (Haines, 1988) and lacustrine phosphatic shales such as the Ediacaran (551–635 Ma) Doushantou Formation of China (Bristow *et al.*, 2009). Ediacaran sulfidic shales with simple discoid fossils such as *Aspidella* (Fig. 1H–I) include intertidal pyritic palaeosols (Retallack, 2013b), comparable with those of modern mangroves and salt marsh (Retallack & Dilcher, 2012). Other Ediacaran fossils, such as *Cloudina* (Hua *et al.*, 2004), and Cryogenian un–named small chambered fossils from limestone (Maloof *et al.*, 2010) appear to have been marine. Ediacaran organic tubular fossils such as *Corumbella* (Warren *et al.*, 2012) and *Ramitubus* (Liu *et al.*, 2008), microbial mats and stromatolites (Noffke &
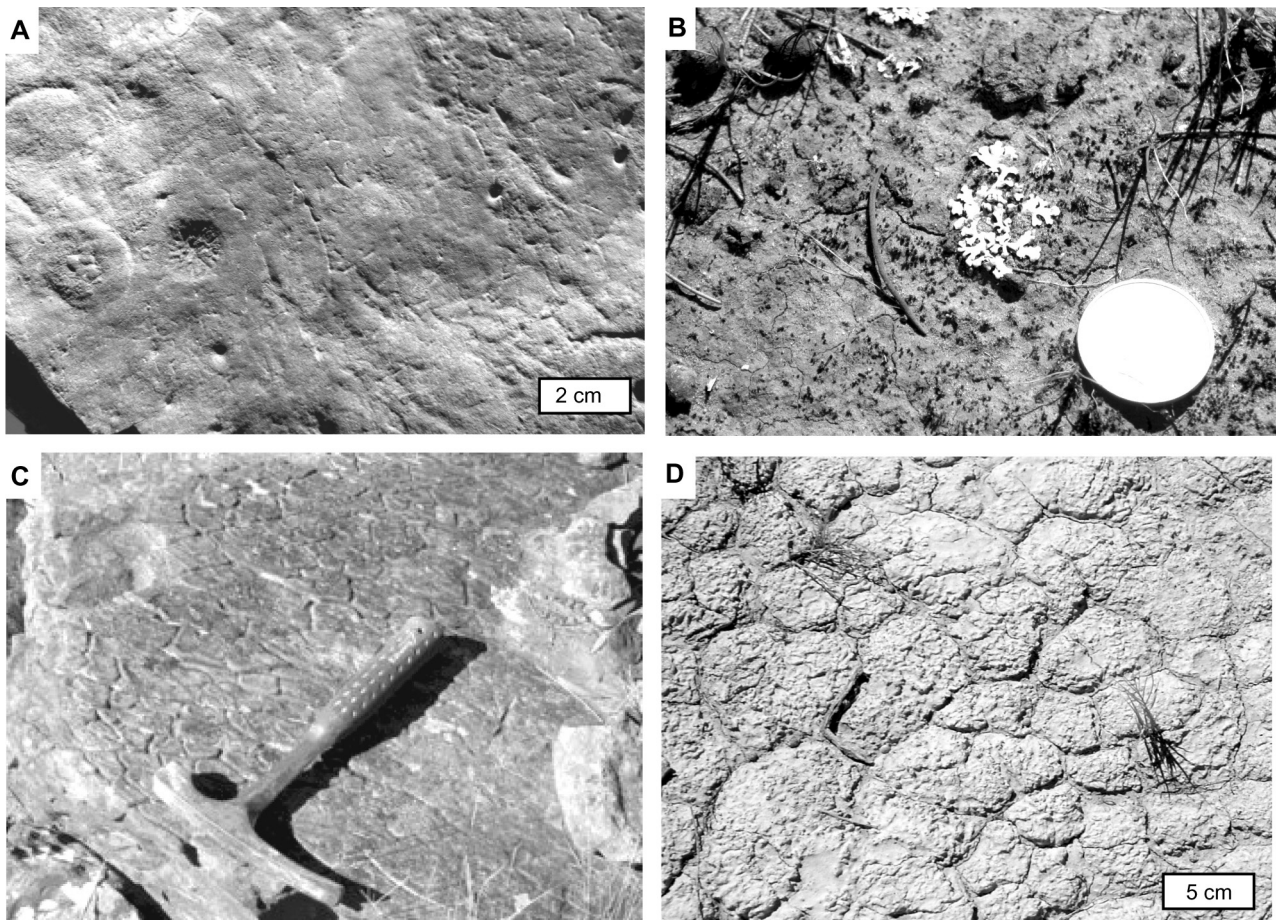

Fig. 3—Fossil (A, C) and modern (B, D) terrestrial microbially–induced sedimentary structures (MISS): (A) *Rivularites repertus* surface with discoids *Hallidayia brueri* (left) and *Rugosoconites enigmaticus* (right), Ediacara Member (Ediacaran) of Crisp Gorge, South Australia: (B) *Xanthoparmelia reptans*, Damara Station, New South Wales; (C) mud cracked *Rivularites repertus* surface in Stirling Range Sandstone (Palaeoproterozoic), Barnett Peak, Western Australia; (D) mud cracked surface of lay with *Microcoleus vaginatus* Black Rock Desert, Nevada. Specimen (A) is on display at the South Australian Museum: others are field photographs.

Awramik, 2013) and a variety of seaweed–like impressions in shales (Yuan *et al.*, 2011) appear to have been aquatic, both marine and lacustrine (Bristow *et al.*, 2009). Ediacaran marine redox and sulfate have been portrayed as very different from modern (Canfield *et al.*, 2007), but Ediacaran palaeosols are in many ways comparable with modern soils (Retallack, 2012b, 2013a, d).

Identification of modern fungi often requires isolation of spores or other microscopic evidence, but most Ediacaran fossils are preserved as molds and casts in which such organic structures are not preserved. A more promising source of biological information is the suggestion of Pirozynski (1976), Redecker *et al.* (2000), and Butterfield (2005) that there is an early Palaeozoic and Precambrian record of fungi among the enigmatic microfossil palynomorphs known as acritarchs (Javaux *et al.*, 2001; Grey, 2005; Lamb *et al.*, 2009; Moczydłowska *et al.*, 2011; Strother *et al.*, 2011). Ediacaran fossils such as *Germinosphaera* (Fig. 1M, 5H) and *Ceratosphaeridium* (Fig. 1N, 5E) and Cryogenian–Mesoproterozoic fossils such as *Tappania* (Fig. 1O, S) are similar to Glomeromycotan chlamydospores and vesicles (Fig. 5A–D: Pirozynski, 1976; Wu *et al.*, 1995, 2005; Walker *et al.*, 2004; Sieverding & Oehl, 2006)). Ediacaran acritarchs also show splitting of a brittle wall (Fig. 5F) and surface ornament (Fig. 5C) like those of modern glomeromycotans. A fragment of a permineralised glomeromycotan lichen has been recorded from above a palaeokarst in the lacustrine lower portion of the Doushatou Formation of China (Yuan *et al.*, 2005; Bristow *et al.*, 2009). Spores and permineralisations comparable with those of Basidiomycota and Ascomycota are conspicuous in

their absence from the fossil record until the Silurian (Berbee & Taylor, 2010). A long Precambrian fossil record of fungi that eventually became mycorrhizae supports the idea that the land was prepared for land plants by long prior evolution of terrestrial Glomeromycota (mycotrophic hypothesis of Pirozynski & Malloch, 1975).

Red sandstone impressions comparable with the Ediacaran fossils from South Australia have also been recognised in pre–Ediacaran rocks, such as the 1250 Ma Pandwa Falls Sandstone of India (Fig. 1P: Williams & Schmidt, 2003), the 1128 Ma Mt John Shale Member of Western Australia (Fig. 1R; McCall, 2006), and 2100 Ma Stirling Range Formation, Barnett Peak, Western Australia (Fig. 1U–V). The Stirling Range fossils are found atop gypsic palaeosols (Retallack, 2012a) on surfaces with old elephant skin and desiccation cracks (Fig. 3C) comparable with modern playa soils (Fig. 3D). The Stirling Range discoidal impressions may have been microbial colonies, and the trail–like markings (*Myxomitodes stirlingensis*) created by the slug–aggregating phase of slime molds (Bengtson *et al.*, 2007). Comparable gypsic palaeosols have recently been found associated with highly oxidised, strata–transgressive filament traces in the 2000 Ma Sugarloaf Quartzite of Wyoming, and a comparable origin is likely for putative trace fossils in the underlying Medicine Peak Quartzite (Kauffman & Steidtmann, 1981). Life on quartz–rich floodplains from the Ordovician back to the Palaeoproterozoic may have included a variety of life forms: lichens, rope–forming and discoid–forming microbes, and slime molds.

PALAEOPROTEROZOIC *DISKAGMA*

Diskagma buttonii is a fossil from the surface (A horizon) of the 2200 Ma Waterval Onder clay palaeosol of South Africa (Retallack *et al.*, 2013a). The Waterval Onder palaeosol has played an important role in research on the Palaeoproterozoic Great Oxidation Event (Rye & Holland, 1998), with estimates from geochemical modelling of a rise at that time to 0.9–5 % atmospheric O_2 (Retallack, 1986; Murakami *et al.*, 2011; Bekker & Holland, 2012) and thus an ozone shield from ultraviolet radiation (Kasting & Catling, 2003). This palaeosol's chemical composition is evidence of temperate humid climate (mean annual temperature 11.3 ± 4.4°C: mean annual precipitation 1489 ± 182 mm: Retallack *et al.*, 2013a). This and other palaeosols nearby indicate atmospheric CO_2 of 6640 +12880/–4293 ppm (0.6%: Sheldon, 2006). The fossils are locally clumped within surface swales of a Vertisol palaeosol, identified from characteristic penecontemporaneous deformation (clastic dikes between swales of mukkara structure: Retallack 1986) and from pronounced geochemical differentiation (phosphorus and copper strain–corrected mass–depletion characteristic of an oxidised biologically active soil: Neaman *et al.*, 2005). These indications of a plausible palaeoenvironment for life are one
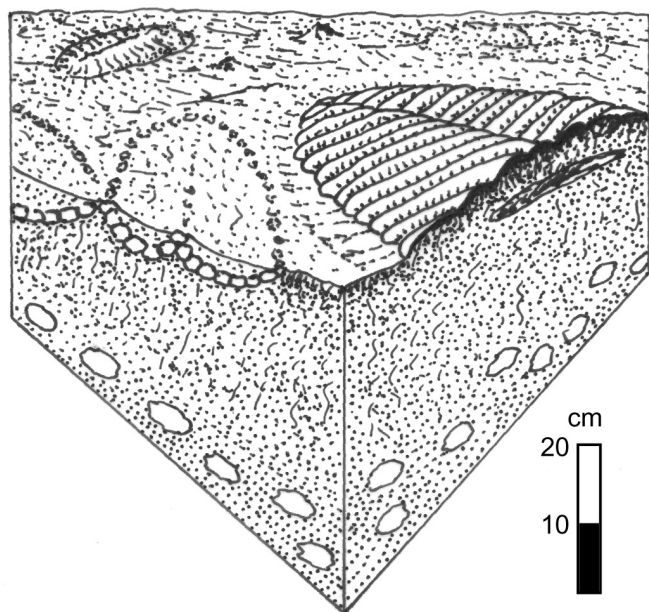

Fig. 4—Reconstruction of *Dickinsonia ovata*, *Phyllozoon hanseni*, and *Aulozoon* sp. in Muru palaeosol from the Ediacara Member (Ediacaran), Bathtub Gorge, South Australia (modified from Retallack, 2007a, 2013d).

of six criteria used to assess the biogenicity of Precambrian fossils recommended by Hoffman (2004). The other criteria are (2) known provenance, (3) same age as the rock, (4) plausible composition (5) taphonomic series, and (6) repeated complexity.

Diskagma buttonii fossils are from fresh rock of a deep highway cutting (criterion 2), and have been recrystallised and metamorphosed to upper greenschist facies like their matrix (criterion 3). Despite metamorphic alteration, total organic carbon of the samples was 0.04 % and its isotopic composition ($\delta^{13}C$) was −25.6 ± 0.08 ‰ (two standard deviations) versus Vienna Pee Dee belemnite standard (criterion 4). Organic outlines of the fossils are accentuated by recrystallised berthierine and opaque oxides and vary in degree of inflation and continuity (criterion 5).

Finally there is the criterion (number 6 of Hoffman, 2004) of repeated complexity. *Diskagma* are small (0.3–1.8 mm long), locally abundant, urn–shaped fossils with a flared rim, and closed below the flare. They show little contrast with their matrix in hand specimens (Fig. 6C), but in thin section their hollow ellipsoidal interior is unusually devoid of opaque debris, unlike the matrix (Fig. 6A–B). Cyclotron x–ray imaging was needed to fully appreciate their form (Fig. 6D, 7A) because they are too big to be contained entirely within a thin section and their matrix is opaque. Especially intriguing are filamentous structures within the apical cup (Fig. 6B), but unfortunately detailed structure there is obscured by metamorphic recrystallisation (Retallack *et al.*, 2013a).

Diskagma is superficially comparable with the living soil organism *Geosiphon* (Fig. 6E), which is a fungus (Archaeosporales, Glomeromycota) with endosymbiotic cyanobacteria (Schüßler & Kluge, 2000). Fungal–cyanobacterial symbioses are commonly called lichens, but most lichens are ectosymbiotic (with phycobiont held by haustorial hyphae), and Hawksworth & Honegger (1994) recommend excluding *Geosiphon* from lichens. The large interior cavity of *Diskagma*, and its size, connecting threads, and soil habitats, are the main points of similarity with *Geosiphon*. Other *Geosiphon*–like fossils with a conspicuous central hollow and radiating basal threads include 1480 Ma *Horodyskia*, which lived in shallow lakes (Retallack *et al.*, 2013b), and the un–named 2083 Ma Franceville fossils (Fig. 1T), which lived in coastal tidal flats or lagoons (El Albani *et al.*, 2010). *Diskagma* differs from all (*Geosiphon*, *Horodyskia* and the Franceville fossils) in its apical cup with poorly preserved filamentous structures, and so remains enigmatic (Retallack *et al.*, 2013a). Although biological affinities of *Diskagma* are uncertain, these fossils reveal the general
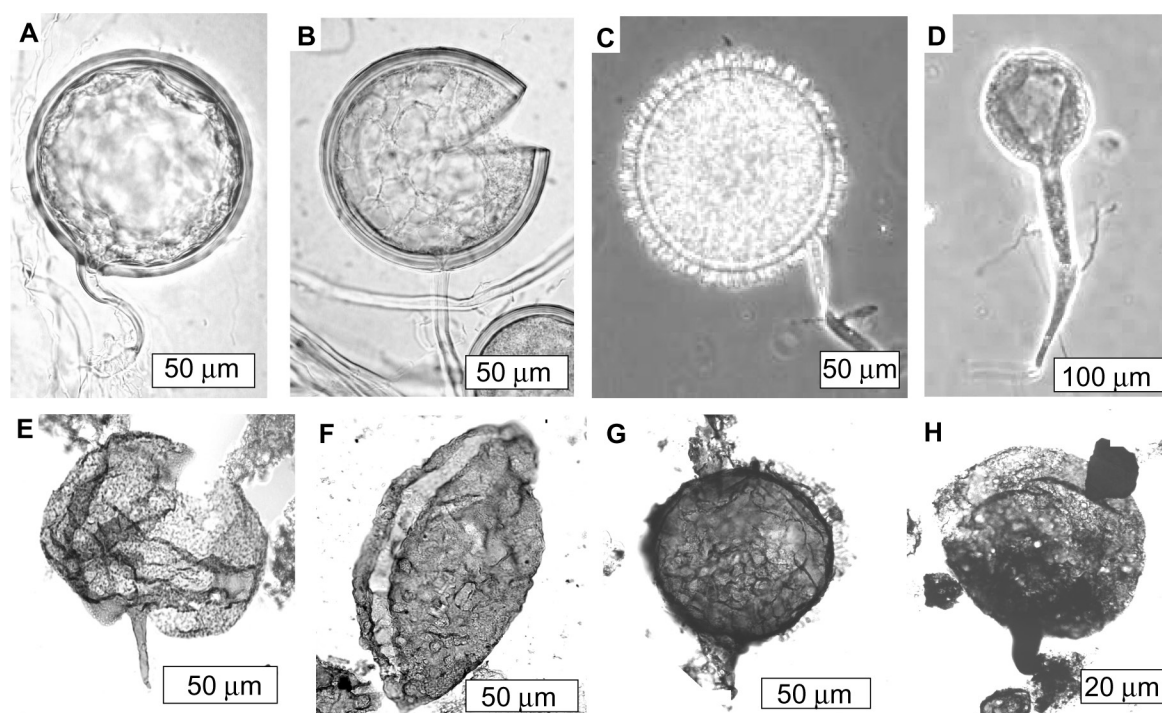

Fig. 5—Modern fungal spores (A–C) and sporiferous saccule (D) and comparable Ediacaran acritarchs (E–H): (A) *Glomus claroideum*, Laukan, Finland: (B) *Glomus intraradices*, Îles de la Madeleine, Quebec, Canada: (C) *Gerdemannia chimonobambusae*, Nan–Tou, Taiwan (Wu *et al.*, 1995; Walker *et al.*, 2004); (D) *Kuklospora kentinensis*, Ping–tong, Taiwan (Wu *et al.*, 2005; Sieverding & Oehl, 2006); (E) *Ceratosphaeridium mirabile*, Wilari Dolomite Member, Tanana Formation, Observatory Hill no., 1 well, northern South Australia (Grey, 2005); (F) *Schizofusa zangwenlongii*, Dey Dey Mudstone, Observatory Hill bore, northern South Australia (Grey, 2005); (G) *Appendisphaera centroreticulata*, Tanana Formation, Munta 1 bore, northern South Australia (Grey, 2005); (H) *Germinosphaera* sp. indet. ABC Range Quartzite, SCYW1a bore, South Australia (Grey, 2005): (A–B) by Yolande Dalpé, (C–D) by Chiguang Wu, and (E–H) by K. Grey, with permission.

appearance of Palaeoproterozoic life on land (Fig. 7B), and provide search images for discovery of more informative material (Fig. 7A).

Such a large and complex fossil as *Diskagma*, is likely to have been eukaryotic, and perhaps the oldest known eukaryote (Knoll *et al.*, 2006), because it predates the marine siphoneous alga *Grypania*, once considered 2110 Ma old (Han & Runnegar, 1992), but redated to 1850 Ma (Schneider *et al.*, 2002). *Diskagma* is also older than current molecular clock estimates for eukaryotes (1600 Ga: Bhattacharya *et al.*, 2009) and fungi (1100 Ga: Blair, 2009; Berbee & Taylor, 2010). Another line of evidence for eukaryotes back 2200 Ma is the biomarker ergosterane (Dutkiewicz *et al.*, 2006), widespread in fungi and algae (Knoll *et al.*, 2007; Moore, 2013). Earlier occurrences of ergosterane back to

2700 Ma (Brocks *et al.*, 2003; Waldbauer *et al.*, 2011) are now suspected as contamination by geologically younger hydrocarbons (Kirschvink & Kopp, 2008).

ARCHAEAN FOSSILS

Thucomyces lichenoides from the 2800 Ga (Schaefer *et al.*, 2010) Carbon Leader of the Central Rand Group near Carletonville, South Africa are tubules 2–3 mm long by 0.5–0.6 mm in diameter (Fig. 1Z–AA; 8A: Hallbauer & van Warmelo, 1974, Hallbauer *et al.*, 1977). They are surprisingly abundant within palisades in growth position on palaeosols, and redeposited in fluvial sandstones (Fig 9B: Minter, 2006; Mossman *et al.*, 2008). Early reaction to *Thucomyces* doubted that they were even fossils. Cloud (1976)
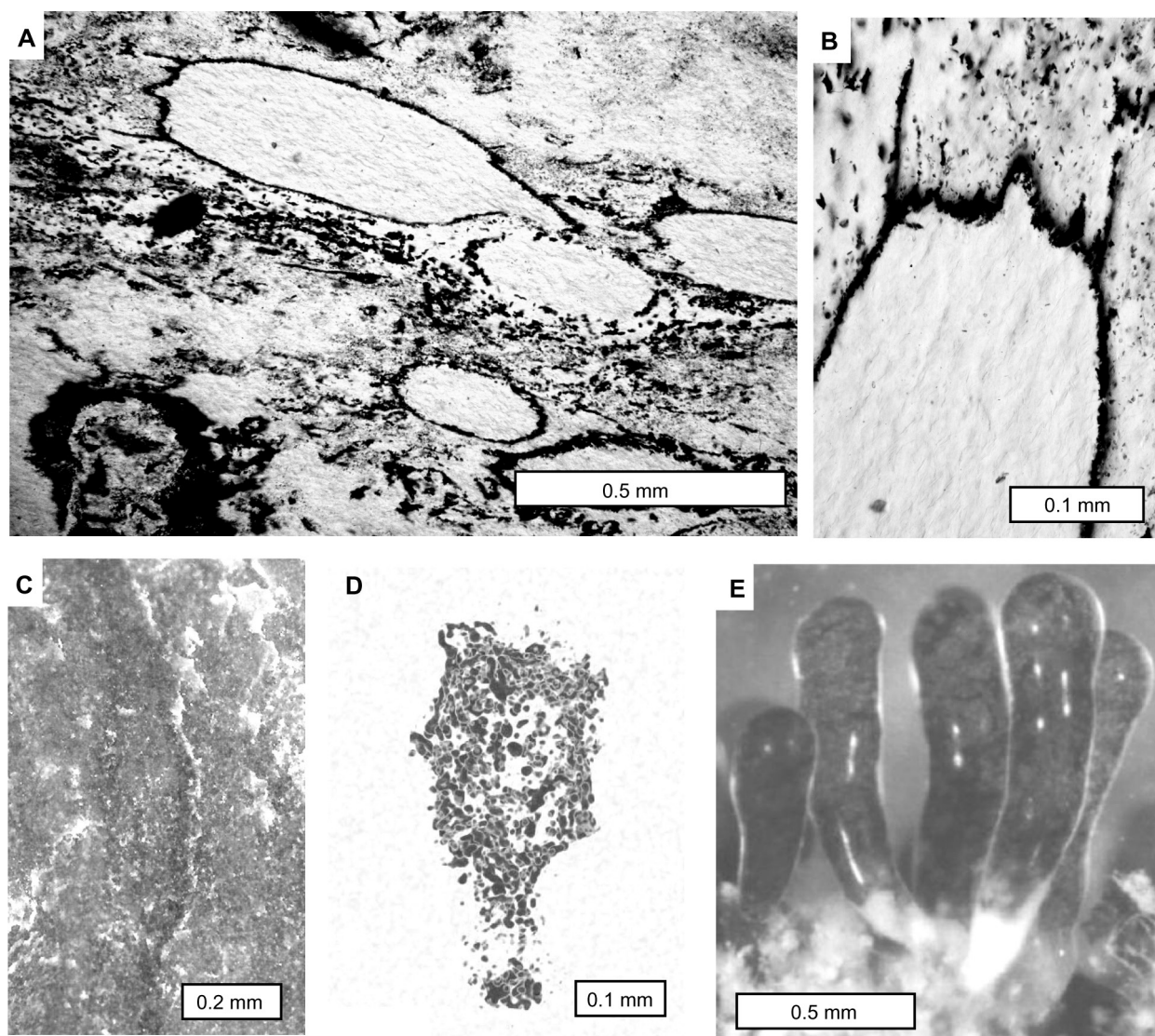

Fig. 6—Urn–shaped fossils in thin section (A–B) and on rock (C), tomographic image (D), and comparable living organisms (E): *Diskagma buttonii*, from Waterval Onder palaeosol in uppermost Hekpoort Basalt (Palaeoproterozoic), near Waterval Onder, South Africa (Retallack *et al.*, 2013a): (D) *Geosiphon pyriformis*, from forest floor, Darmstadt, Germany. Image D courtesy of Arthur Schüβler.

considered them artefacts of bubbling HF acid used to extract them from the matrix, and Barnicoat *et al.* (1997) considered them blebs of mobilised postmetamorphic hydrocarbon. However, *Thucomyces* palisades in place within thin sections and polished slabs are cut by metamorphic veins (MacRae, 1999), and also have been observed redeposited within sediments on the same stratigraphic horizons (Mossman *et al.*, 2008). Oxygen and hydrogen isotopic composition of carbon compounds of *Thucomyces* rules out metamorphic remobilization (Grové & Harris, 2010).

Clues to biological affinities of *Thucomyces* include its very light and variable carbon isotopic compositions averaging–28.1 ‰ (mostly ranging from 27.1 to–32.8 ‰, but including two outliers of–22.4 to–22.9 ‰: Hoefs & Schidlowski, 1967). Organic matter of *Thucomyces* also has pentose/hexose ratios of 1, and chlorophyll–bacteriochlorophyll derivatives such as pristane and phytane of photosynthetic organisms (Prashnowsky & Schidlowski, 1967). The trace elements bioaccumulated by, or biofilmed onto, *Thucomyces* include native gold and uranium (MacRae, 1999; Mossman *et al.*, 2008). *Thucomyces* has complex vertical internal partitions (Fig. 9A), and shows little similarity with living lichens (Brodo *et al.*, 2001) or *Geosiphon* (Schüßler & Kluge, 2000). This irregular internal structure is comparable with columnar biofilms (Hall–Stoodley *et al.*, 2004), which develop curtain–like seams with changing water level (Fig. 9B). As a biofilm, *Thucomyces* would not have been a single organism, but rather a microbial community including photosynthetic and methanogenic components, judging from chemical composition (Hoefs & Schidlowski, 1967; Prashnowsky & Schidlowski, 1967). Furthermore, drab palaeosols and uraninite clasts in palaeochannels are evidence for anaerobic metabolism of these terrestrial biofilms (Minter, 2006; Mossman *et al.*, 2008).

The microfossil *Witwateromyces conidiophorus* (Fig. 1AB) associated with *Thucomyces* biofilms has been interpreted as fungal conidiophores (Hallbauer *et al.*, 1977). If so, it would be surprisingly early evidence of eukaryotes (Bhattacharya *et al.*, 2009; Blair, 2009; Berbee & Taylor, 2010), but comparable spore chains are also found in prokaryotic Actinobacteria, such as *Dactylosporangium fulvum* (Shomura *et al.*, 1986) and *Actinocorallia herbidum* (Iinuma *et al.*, 1994). Decomposers such as fungi or actinobacteria must have been present in Precambrian palaeosols with organic compounds or other geochemical evidence of life, because organic content of Precambrian palaeosols is as low as in Phanerozoic palaeosols (Retallack & Mindszenty, 1994). When mechanisms of decay are suppressed, for example by waterlogging, living soils become peats, and then after burial, become coals (Retallack, 1997).

Also plausibly terrestrial are microfossils from the 3000 Ma Farrel Quartzite of Western Australia (Sugitani *et al.*, 2007, 2009). The microfossils come from black cherts interbedded with evaporite pseudomorphs of likely coastal lagoon to playa habitats, stratigraphically above fluvial sandstones and below marine shales (Sugitani *et al.*, 2003, 2006). The Farrel microfossils are surprisingly large (>15 μm) and complex (Fig. 1AD, Fig. 10A–B), as well as diverse, with spheroidal cells of different sizes and wall types, both solitary and aggregated, and large spindle–shaped structures clustered with attached filaments. Carbon isotopic composition of individual Farrel microfossils is also varied, ranging from $\delta^{13}C$ –33.8 ‰ to –44.2 $\delta^{13}C$ ‰ for spheroids, and from $\delta^{13}C$ –35.8 ‰ to –40.5 $\delta^{13}C$ ‰ for spindles (House *et al.*, 2013). The spindles with filaments are similar in morphology with sporangia of filamentous Actinobacteria, such as *Planomonospora alba* (Fig. 9C) and *Streptosporangium roseum* (Fig. 9D). As actinobacterial decomposers their
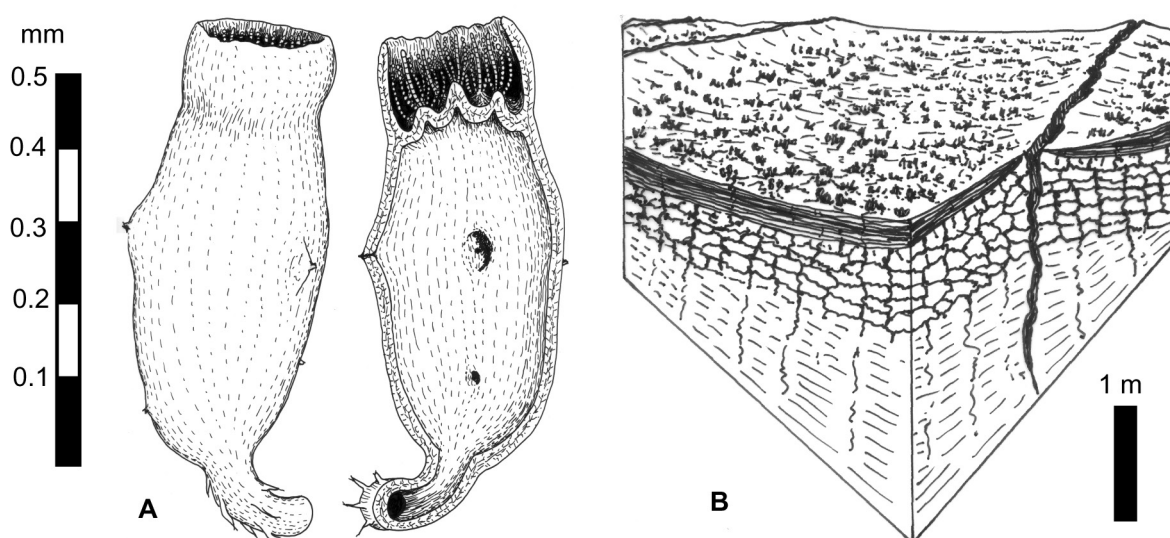

Fig. 7—Reconstruction of *Diskagma buttonii* (A) and its cover of the Waterval Onder clay palaeosol (B), a deeply cracked Vertisol palaeosol.
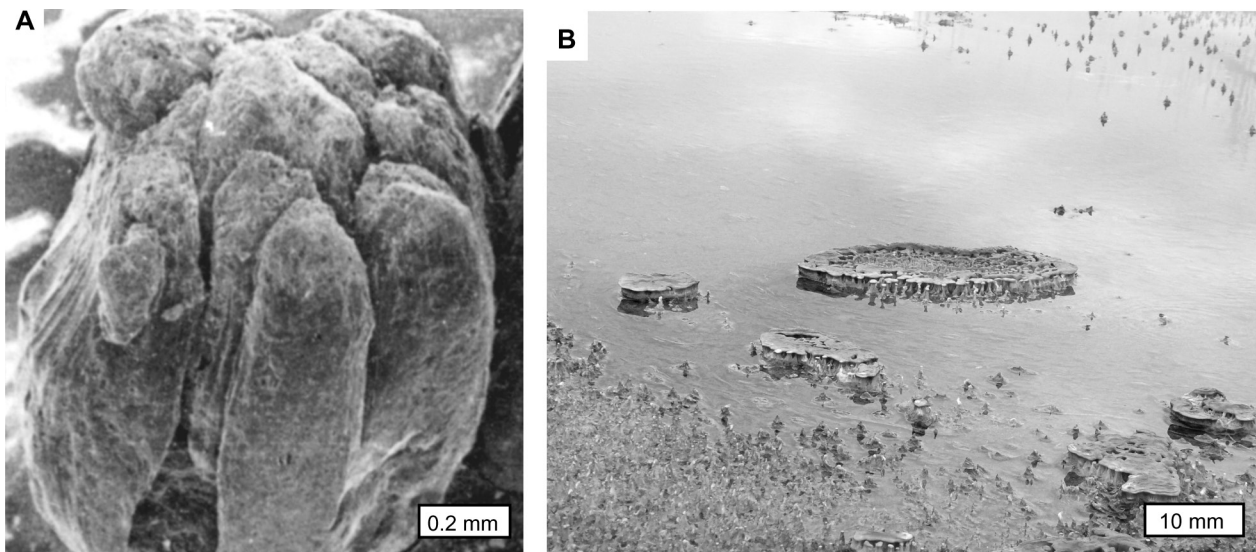
Fig. 8—Palisade fossils (A) and comparable columnar biofilm (B): (A) *Thucomyces lichenoides* from Carbon Leader (NeoArchaean) from Carletonville, South Africa; (B) columnar biofilm from Biscuit Basin, Yellowstone National Park, Wyoming, USA. Image A is courtesy of Dieter Hallbauer and B from Paul Stoodley, with their permission.

unusually light and varied isotopic composition may reflect a diet of spheroidal methanogens and photosynthetic bacteria. Actinobacteria are a key component of a bacterial clade called Terrabacteria, because of their resistance to desiccation, ultraviolet radiation, and high salinity. Terrabacteria date back to 3180 Ma using molecular clocks (Battistuzzi & Hedges, 2009). The alternative idea of House *et al.* (2013) that the Farrel microfossils were cosmopolitan plankton because of the occurrence of comparable spindles in South Africa (Walsh 1992), is unlikely considering the depositional setting and sessile, clustered, filamentous attachment of the spindles in

3416 Ma cherts of South Africa (Walsh 1992) and 3000–3420 Ma cherts of Western Australia (Sugitani *et al.*, 2003, 2006, 2013).

The Farrel microfossils can be contrasted with marine small spheroids and filaments permineralised in the 3465 Ma Apex Chert of Western Australia (Schopf & Packer, 1987). These fossils have been disputed because some are poorly preserved (Brasier *et al.*, 2002), but such taphonomic variation is evidence for, not against, biogenicity (Hoffman, 2004), especially in view of other evidence from Raman spectra and confocal laser scanning that they were fossils (Schopf
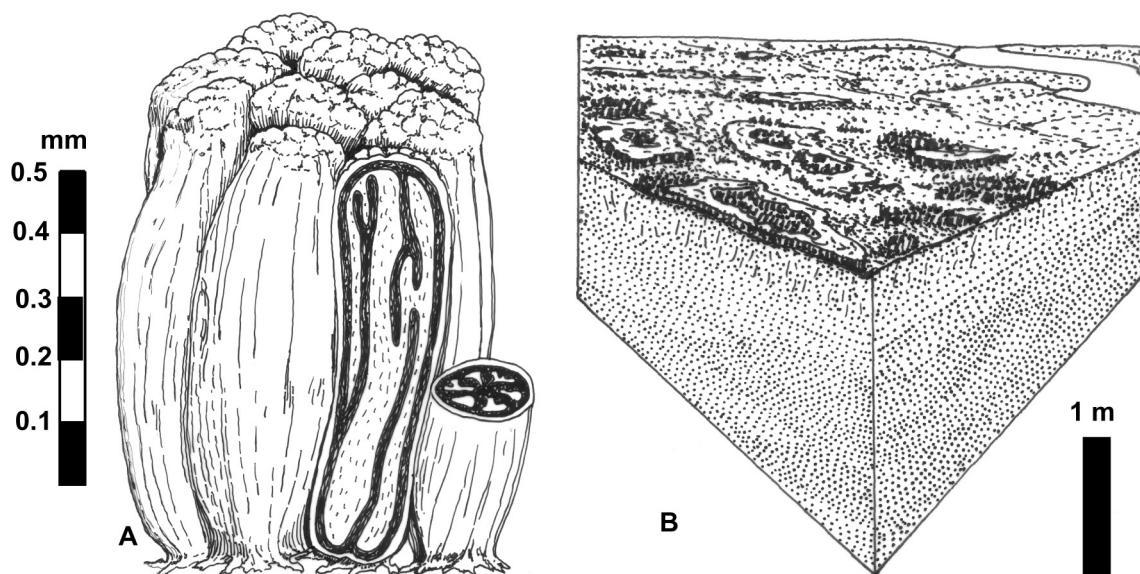

Fig. 9—Reconstruction of *Thucomyces lichenoides* (A: modified from Hallbauer *et al.*, 1977) and its fluvial floodplain environment (B: after Mossman *et al.*, 2008).

et al., 2007). The reinterpretation of the Apex Chert as a hydrothermal vein (by Brasier *et al.*, 2002) is not credible either, considering mineralogical studies revealing formation temperatures below 150ºC, which is within microbial tolerances (Pinti *et al.*, 2009). My ongoing remapping of the Apex Chert locality, as well as other putative hydrothermal veins (Lindsay *et al.*, 2005), has failed to demonstrate tapering or branching veins, or hydrothermal alteration, but instead confirmed the angular unconformity and palaeosol widespread in this region of Western Australia (Buick *et al.*, 1995). The Farrel and Apex microfossil assemblages may represent distinct terrestrial and marine microbiotas at the dawn of the useful fossil record of life on Earth. The oldest records of life in this region are stromatolites and microbial mats dated at some 3490 Ma (van Kranendonk *et al.*, 2003, 2008).

ORIGIN OF LIFE ON LAND

Metaphors of colonization or invasion are commonly used to describe early life on land (Retallack, 2012c), either 3180 million years ago for microbes (Battistuzzi & Hedges, 2009), or 472 Ma for land plants (Davies & Gibling, 2010), because the underlying assumption is that life originated in the sea and found its way onto land later (Bernal, 1961). Especially favoured locations for the origin of life are seaside ponds (Bernal, 1961), deep–sea black smokers (Nisbet & Sleep, 2001) or floating pumice (Brasier *et al.*, 2011). These locations suffer major theoretical drawbacks, because the uniform aqueous, neutral pH, buffered Eh, low salinity environment of the sea tends toward chemical equilibrium, but complex and variable environments are required to synthesize and preserve proteins and nucleic acids (Cairns–Smith, 1971). Arguments for marine origins of life stress the smallness and
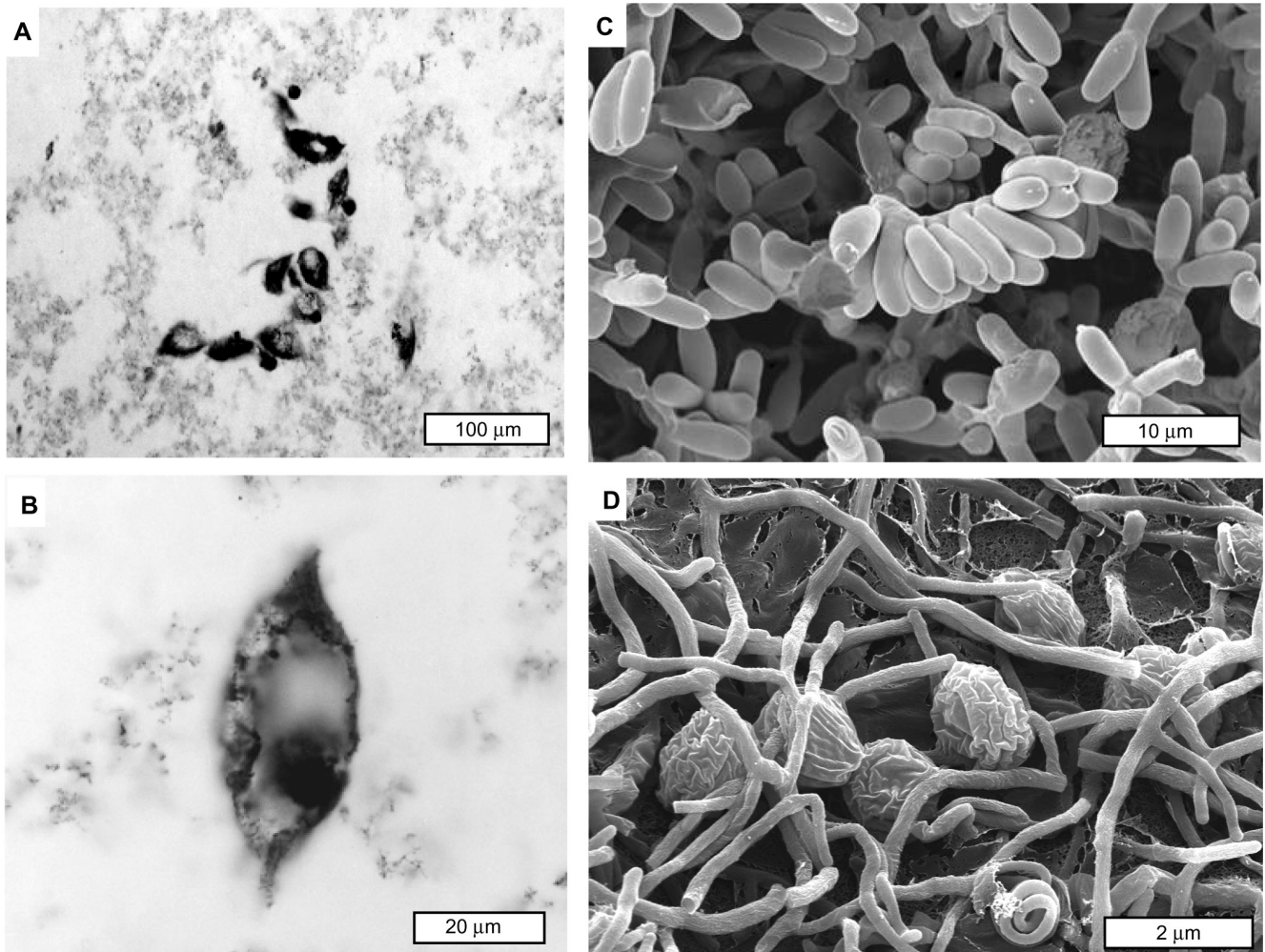

Fig. 10—Discoidal un–named microfossils (A, B) and comparable Actinobacteria (C, D); (A–B) unamed clustered discoidal fossils from the Farrel Sandstone (MesoArchaean) Mt Grant, Western Australia; (C), *Planomonospora alba* ; (D) *Streptosporangium roseum*. Images A–B from Sugitani *et al.* (2007); C from John Innes center, UK with permission from Kim Findlay, Emma Sherwood and Mervyn Bibb, and D, from German Collection of Microorganisms and Cell Cultures, with permission of Matt Nolan and Hans–Peter Klenk.

ephemerality of the seaside ponds (Bernal, 1961) or vesicular cavities of pumice (Brasier *et al.*, 2011) or deep–sea vent sulfides (Nisbet & Sleep, 2001). Small volumes are necessary to thwart chemical equilibrium and to meter nutrient supply, two essential components of life and metabolic reactions (Cairns–Smith, 1971). The pore spaces between mineral grains of soils take these advantages to extreme: millions of warm little ponds or vesicles in every teaspoonful of soil. The water content of soils varies from fully irrigated after heavy rain to small menisci between grains in a soil close to permanent wilting point. These tiny menisci accumulate clays and nutrient cations from the weathering of mineral grains, and varying acidic to neutral pH, hydrous to desiccated conditions, and high to low cationic concentration, at different times after rain storms (Retallack, 2007b). Especially important for metabolic activity are strong Eh gradients, which would have been suppressed in Archaean oceans with abundant reduced manganese and iron (Kirschvink & Weiss, 2002). Results of the Viking Martian mission biological experiments and redox gradients of Martian soils (Benner, 2010), have led to the proposal that life is more likely to have evolved on a soil planet like Mars, than a water planet like Earth (Kirschvink & Weiss, 2002; Benner, 2010).

In addition, soils producing clay by weathering and organic matter by abiotic synthesis would be selected by natural selection (Retallack, 2007b). Rain and rivers would selectively erode the least clayey and organic soils, leaving planetismals of the early Solar System covered with soil similar to carbonaceous chondritic meteorites. High temperature inclusions of carbonaceous chondrites are dated radiometrically at 4566 Ma, and their low temperature components no more than 50–60 Ma younger than this from radiometric dating of calcite veins and clays (Birck & Allègre, 1988; Endress *et al.*, 1996). Carbonaceous chondrites also show other features of soils, including weathering rinds around pyrogenic pyroxene and olivine, and soil shrink–swell (sepic plasmic) microfabrics (Bunch & Chang, 1980). Carbonaceous chondrites can be considered fragments of the earliest palaeosols of the Solar System (Retallack, 2007b). There are thus theoretical reasons to consider soils as possible incubators of life.

CONCLUSIONS

Although fossils in Precambrian palaeosols remain few, enough are known to suggest life on land well back into the Archaean (Buick *et al.*, 1995; Sugitani *et al.*, 2013), and as old as comparable evidence for life in the sea (van Kranendonk *et al.*, 2003, 2008; Schopf *et al.*, 2007). The persistent bias against interpreting Precambrian fossils as non–marine is effectively broken, but understanding of differences between life on land and in the sea at various times of the Precambrian remains incomplete. Better understanding of life on land in the Precambrian will be needed to understand atmospheres,

landscapes and tectonics of the early Earth (Retallack, 2007b). There is now evidence for life on both land and sea back to the beginnings of the useful fossil record in lightly metamorphosed sequences of Western Australia (van Kranendonk *et al.*, 2003, 2008; Schopf *et al.*, 2007; Sugitani *et al.*, 2013) and South Africa (Walsh, 1992; Noffke & Awramik, 2013). Thus the fossil record no longer strongly supports the view that life originated in the sea (Bernal, 1961; Nisbet & Sleep, 2001; Brasier *et al.*, 2011). Theoretical arguments for the origin of life in soil include its changeable conditions in time and space, and thus metered supply of nutrients and water. Soils are the main locus of clay and organic matter production now and in the distant past, and this colloidal manufacture is an important element of natural selection against destruction from erosion (Retallack, 2007b). Complex clayey and organic soils of planetismals during the early formation of the Solar System may be represented by carbonaceous chondrites (Bunch & Chang, 1980). Such naturally selected clayey and organic substrates are ideal sites for the origin of life.

> "Was it for this the clay grew tall?
> O what made fatuous sunbeams toil
> To break earth's sleep at all?"
> (Wilfred Owen, from Stallworthy, 1994)

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