

CRITERIA FOR DISTINGUISHING MICROBIAL MATS AND EARTHS

GREGORY J. RETALLACK

Department of Geological Sciences, University of Oregon, 1275 East 13th Avenue, Eugene, Oregon 97302, USA
e-mail: gregr@uoregon.edu

ABSTRACT: Microbial earths are communities of microscopic organisms living in well-drained soil. Unlike aquatic microbial mats and stromatolites, microbial earths are sheltered from ultraviolet radiation, desiccation, and other surficial hazards within soil cracks and grain interstices. Currently, such ecosystems are best known in small areas of unusually cold, hot, or saline soils unfavorable to multicellular plants and animals. During the Precambrian, microbial earths may have been more widespread, but few examples have been reported. This review outlines a variety of features of modern microbial earths that can be used to distinguish them from aquatic microbial mats and stromatolites in the fossil record. Microbial earths have vertically oriented organisms intimately admixed with minerals of the soil, whereas microbial mats are laminated and detachable from their mineral substrate as flakes, skeins, and rollups. Microbial earths have irregular relief, healed desiccation cracks, and pressure ridges, whereas microbial mats have flexuous, striated domes, and tufts. Microbial earths form deep soil profiles with downward variations in oxidation, clay abundance, and replacive nodular subsurface horizons, whereas microbial mats form as caps to unweathered, chemically reduced sedimentary layers. Microbial earths develop increasingly differentiated soil profiles through time, whereas microbial mats build upward in laminar to domed increments. Microbial earths are found in nonmarine sedimentary facies, whereas microbial mats form in lacustrine, floodplain, and marine sedimentary facies. Microbial mats and stromatolites are known back to the oldest suitably preserved sedimentary rocks in the 3458 Ma Apex Chert and 3430 Ma Strelley Pool Formation (respectively) of the Pilbara region of Western Australia. The geological antiquity of microbial earths extends back to 2760 Ma in the Mount Roe paleosol of the Hamersley Group near Whim Creek, Western Australia.

KEY WORDS: microbial mat, microbial earth, stromatolite, Precambrian, paleosol

INTRODUCTION

Microbial earth was defined by Retallack (1990, 1992) as a terrestrial ecosystem of microscopic organisms in well-drained soils (Fig. 1B). This review outlines criteria for distinguishing microbial earths from microbial mats (Figs. 1C, 2A), from periphyton of salt marsh, marsh, and fen (Fig. 2B), and from biofilms of stromatolites (Fig. 2C, D), which are aquatic (marine, lacustrine, and wetland) microbial communities (Reid et al. 2000, Noffke et al. 2001a, Kahle 2007, Takashima and Kano 2008, Reuter et al. 2009). Other distinct communities include microbial rocklands (Retallack 1992) and marine endolithic communities (Chazottes et al. 2009, Santelli et al. 2009), which colonize indurated rock surfaces. In the terminology of Retallack (1992) for communities of well-drained soils, megascopic forms such as lichens, mosses, and liverworts mark polsterlands, and small herbaceous tracheophytes (such as the lycopsid resurrection plant *Selaginella lepidophylla*) mark brakelands. Microbial earths and polsterlands are seldom extensive today, but they form patches within angiospermous desert shrublands (Fig. 1B). Nevertheless, the concept of microbial earth is experimentally useful in evaluating modern ecological and physical properties of the microbial contribution to these tracheophyte communities (Hu et al. 2002). Microbes and lichens become more prominent in more disturbed, arid, and frigid areas, where they cover the surface and also live between grains deep within soil (Belnap 2003, Houseman et al. 2006).

A clear concept of microbial earth and their soils is needed to establish the evolutionary history of these ecosystems, before evolution of lichens, liverworts, mosses, and vascular land plants. The Middle Cambrian (510 Ma) appearance of liverworts or mosses, and a Late Ordovician or Early Silurian (450–440 Ma) appearance of vascular land plants is supported by palynological (Nohr-Hansen and Koppelhus 1988, Strother 2004, Beck and Strother 2008) and plant fragment isotopic studies (Tomescu et al. 2009), as well as by studies of rooting structures in paleosols (Retallack 1988, 2008, 2009a). Unnamed permineralized lichens from phosphorites immediately overlying a paleokarst paleosol in the Ediacaran (580 Ma; Condon et al. 2005) Doushantou Formation of China have pyriform terminal

structures interpreted as spores or vesicles of a zygomycotan lichen with coccoid cyanobacterial photosymbionts (Yuan et al. 2005). Gold-permineralized podetiate lichens (*Thucomyces lichenoides*), 4–5 mm long and 1–2 mm in diameter, in the Carbon Leader of the Witwatersrand Supergroup near Johannesburg, South Africa (Hallbauer and van Warmelo 1974, Hallbauer et al. 1977), are no younger than the sensitive high-resolution ion microprobe U-Pb date of 2764 ± 5 Ma for authigenic xenotime of the Central Rand Group (Kositcin and Krapež 2004). Their organic matter has isotopically light carbon, pentose/hexose ratios of 1, and chlorophyll derivatives such as pristane and phytane (Prashnowsky and Schidlowski 1967). These fossils are cut by metamorphic veins, and so they are indigenous to the rock rather than contaminants (MacRae 1999). Furthermore, these Archean megascopic lichens form dense palisade-like colonies atop gray-green kaolinitic paleosols of fluvial floodplains (Minter 2006, Mossman et al. 2008). This sparse fossil record rests on rare and exceptionally preserved fossils, but this paper searches for wider recognition of lichen polsterlands and microbial earths in Precambrian paleosols.

Modern microbial earths and polsterlands have distinctive megascopic surface textures (Fig. 3) that may enable their recognition in the fossil record, similar to microbially induced sedimentary structures (MISS; Noffke et al. 2001a, 2001b; Noffke 2008, 2009), “old elephant skin” (OES; Bottjer and Hagadorn 2007), and textured organic surfaces (TOS; Gehling and Droser 2009). However, surface textures are not in themselves sufficient to identify microbial earths. Microbial filaments and other petrographic textures deep within paleosols are needed, as documented for Ediacaran (Retallack 2011), Cambrian (Retallack 2008), and Cretaceous paleosols (Simpson et al. 2010). In addition, geochemical analyses and depth functions are indications of weathering and life in Precambrian paleosols (Retallack 1986). For example, isotopically light organic carbon of presumed photosynthetic origin has been reported in a 800 Ma paleosol below the Torridonian Supergroup in Scotland (Retallack and Mindszenty 1994), on 1300 Ma paleokarst in the Mescal Limestone of Arizona (Beeunas and Knauth 1985, Vahrenkamp et al. 1987), and from a 2300 Ma paleosol below the Huronian Supergroup near Elliott Lake, Ontario (Mossman and Farrow 1992). Remarkably light C-isotope values indicative of

Microbial Mats in Siliciclastic Depositional Systems Through Time
SEPM Special Publication No. 101, Copyright © 2011
SEPM (Society for Sedimentary Geology), ISBN 978-1-56576-314-2, p. 139–152.

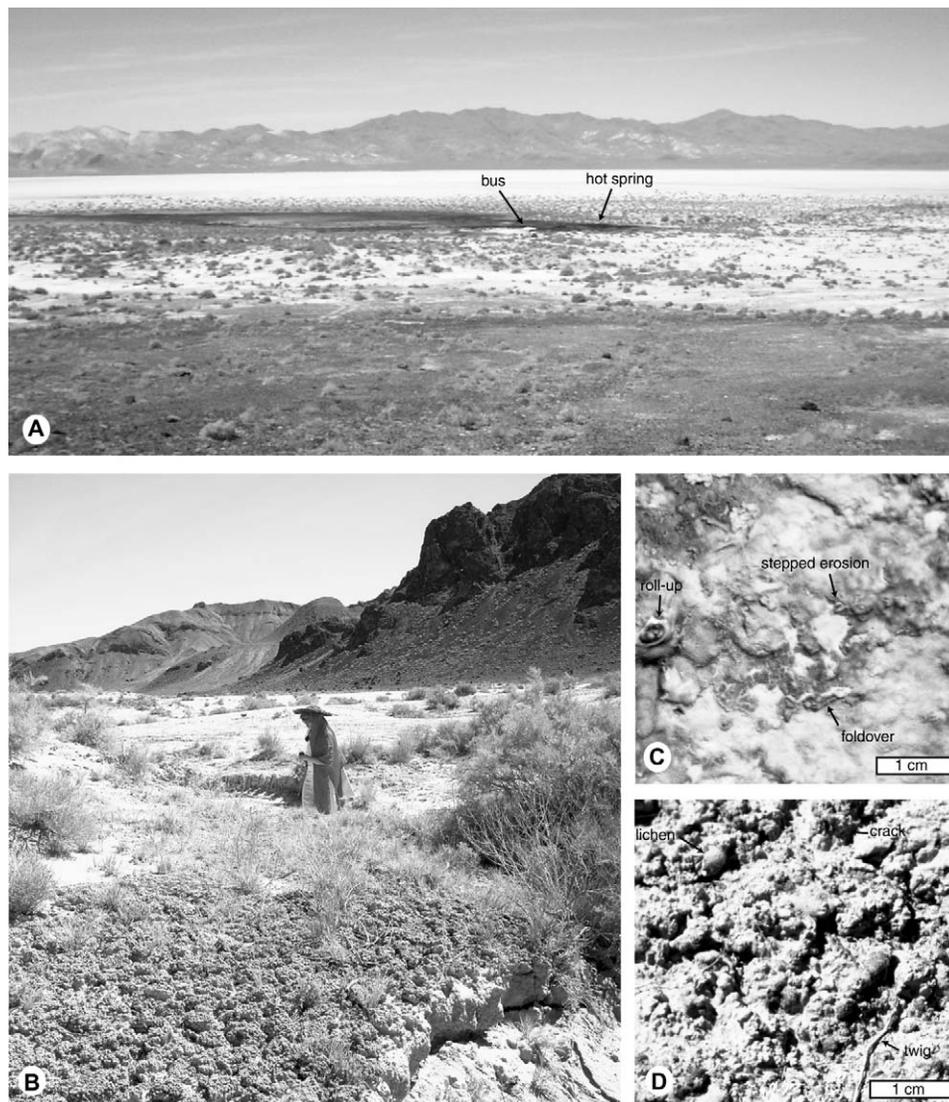


FIG. 1.—Modern patches of microbial earth and mat around a hot spring south of Black Rock, Nevada, USA (40.973645°N, 119.008876°W): (A) overview of hot spring and desert playa from alluvial fan flanking Black Rock, (B) microbial earth erosional profile and shrubs of shadscale saltbush (*Atriplex confertifolia*) and greasewood (*Sarcobatus vermiculatus*), (C) cyanobacterial mats, rollup, and stepped erosion where disturbed by livestock, and (D) button lichen (*Toninia*) polster land with healed desiccation cracks.

methanotrophs have been recorded from the 2760 Ma Mount Roe paleosol of Western Australia (Rye and Holland 2000), and isotopically heavy C-isotope values have been found, as in hypersaline microbes, from the 2600 Ma Schagen paleosol, South Africa (Watanabe et al. 2000, 2004). More general arguments for Precambrian life on land back to at least 800 Ma have come from widespread deeply weathered quartz sandstones (Dott 2003), complex clays (Kennedy et al. 2006), and carbonate isotopic compositions (Knauth and Kennedy 2009). These lines of evidence for Precambrian life on land require laboratory analyses, but the principal aim of this paper is to develop criteria for recognition of microbial earths in the field.

A NOTE ON TERMINOLOGY

The term microbial earth was coined by Retallack (1990) as an ecosystem within modern and ancient, well-drained, living soils

lacking megascopic vegetation, such as microbial consortia (lichens or other megascopic microbial aggregates), nonvascular plants (liverworts, hornworts, and mosses), or vascular land plants (tracheophytes). The term was patterned after cryptogamic earth (Wright and Tucker 1991), which differs in containing cryptogams (lichens, fungi, liverworts, or other embryophytes, and ferns or other pteridophytic tracheophytes). Taxonomic problems also arise from general comparable terms, such as algal mat (Golubic and Hofmann 1976) or cryptalgal fabric (Aitken 1967), which imply eukaryotic algae, when the main contributors are prokaryotic cyanobacteria. Although many cyanobacteria are aquatic (Noffke 2010), as many as 20 different taxa have been identified in single desert soils using 16S ribosomal ribonucleic acid (rRNA) genes (Garcia-Pichel et al. 2001) in abundances up to $8 \pm 6 \times 10^5$ active cells per gram of soil (Garcia-Pichel et al. 2003). Cyanobacteria can emerge from dormancy in soils after as long as 70 years (Bristol 1919) and play a significant role in



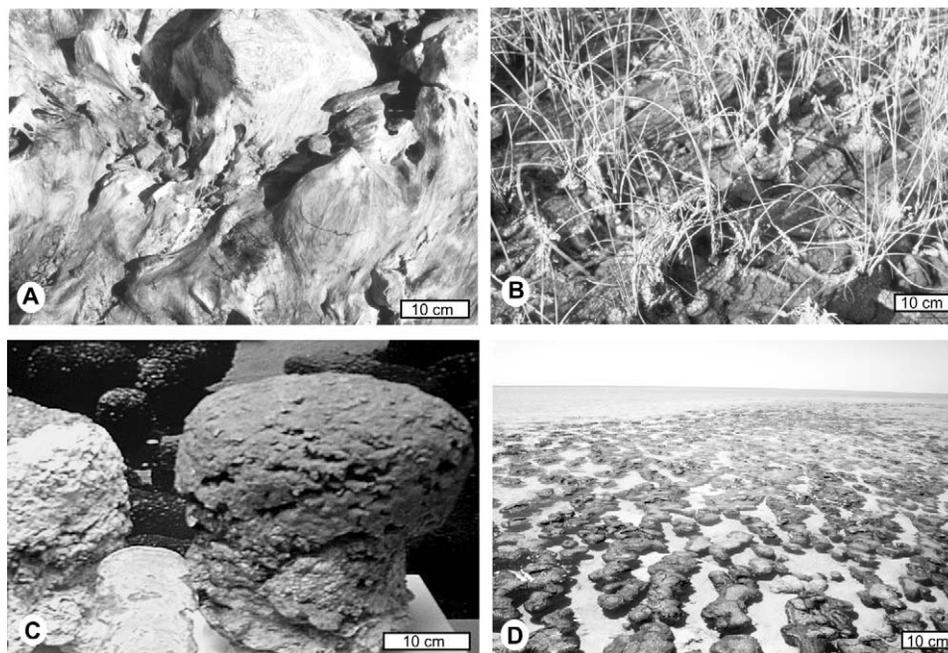


FIG. 2.—Modern microbial mats: (A) cyanobacterial mats and skeins draping sandstone cobbles in dry creek bed near Otematata, New Zealand (44.575046°S, 170.225459°E), (B) cyanobacterial scum (periphyton) in freshwater marsh of spikerush (*Eleocharis cellulosa*), Everglades National Park, Florida, USA (25.365273°N, 80.89593°W), (C, D) calcareous stromatolites from intertidal zone of Hamelin Pool, Shark Bay, Western Australia (26.400467°S, 114.158919°E). Image C is from display of Western Australian Museum, Perth, and includes a sawn cross section of a stromatolite lower left.

chemical weathering (Beraldi-Campesi et al. 2009). A taxonomically neutral term is needed for both modern and fossil microbial earths, because biological affinities of the microbes are often problematic or indeterminable.

A considerable depth (centimeters to meters) of poorly laminated, weathered, living soil is implied by the term “earth,” sometimes including subsurface carbonate nodules also of microbial origin (Monger et al. 1991). Other comparable community terms differ in implying thin surfaces, crusts, or laminations: biological soil crust (Belnap 2003), cryptobiotic soil crust (Belnap and Harper 1995), microbiotic soil crust (Eldridge and Greene 1994), stromatolite (Greek for “layered rock”; Kazmierczak and Altermann 2002, Altermann 2004, Allwood et al. 2007), microbial mat (Schieber 1999), microbialite (Sheehan and Harris 2004), biofilm (Costerton 2007), OES (“old elephant skin” of Bottjer and Hagadorn 2007), and TOS (“textured organic surfaces” of Gehling and Droser 2009). Mats, crusts, skins, and biofilms are thin by definition, and they do not do justice to the depth of microbial colonization of well-drained soils, which can extend many meters (Belnap 2003). Biological soil crusts are defined independent of taxa present and can include land plants (embryophytes) excluded for microbial earths. Microbially induced sedimentary structures (MISS of Noffke et al. 2001a, 2001b) could include all of the aforementioned names, because the phrase does not imply thickness or organization. However, MISS has been defined to include only siliciclastic aquatic depositional environments, and not the chemical or erosional environments of stromatolites and paleosols (Noffke 2010, p. 11). Microbial earths are a form of ecosystem within soils, preserved in both carbonate paleosols (Beeunas and Knauth 1985, Watanabe et al. 2000) and siliciclastic paleosols (Retallack 1986, Retallack and Mindszenty 1994), and they are amenable to the geochemical and petrographic profiling techniques of paleopedology

(Retallack 1990). In essence, microbial earths occupy a volume of soil, whereas microbial mats and crusts are surficial phenomena of a variety of habitats. Microbes of well-drained soil shelter between grains from ultraviolet radiation, desiccation, and other surficial hazards, whereas microbial mats are sheltered and hydrated by ephemeral or permanent water (Belnap 2003, Noffke 2010).

MATERIALS AND METHODS

This work involved fieldwork in the following regions with modern microbial earths: Black Rock Desert, Nevada (Fig. 1B, D); Canyonlands National Park, Utah; Death Valley National Park, California (Fig. 3F); Petrified Forest National Park, Arizona (Fig. 3E); Kalbarri National Park, Western Australia; Flinders Ranges National Park, South Australia; and Lake Mungo National Park, New South Wales, Australia (Fig. 3B–D). Summer drainage of Lake Dorena, near Cottage Grove, Oregon, afforded views of early stages in cracking and cyanobacterial colonization of soil (Fig. 3A). My impressions of microbial mats, periphyton, and stromatolites are informed by observations in Yellowstone National Park, Wyoming; Black Rock Desert, Nevada (Fig. 1C); Everglades National Park, Florida (Fig. 2B); Lake Thetis, Western Australia; Hamelin Pool, Western Australia (Fig. 2C, D); and seasonally dry streams near Otematata, on the South Island of New Zealand (Fig. 2A).

Ancient examples of microbial mats and stromatolites are not a focus of this research because they are widespread and well known (Schieber 1999, Altermann 2004, Allwood et al. 2007). Insights into microbially induced sedimentary structures were gained from observations of rocks associated with the Willamette flora in the Fisher Formation (30 Ma), near Eugene, Oregon (Retallack et al. 2004); in the Mount McRae Shale and Brockman Iron Formation (2470 Ma), in and

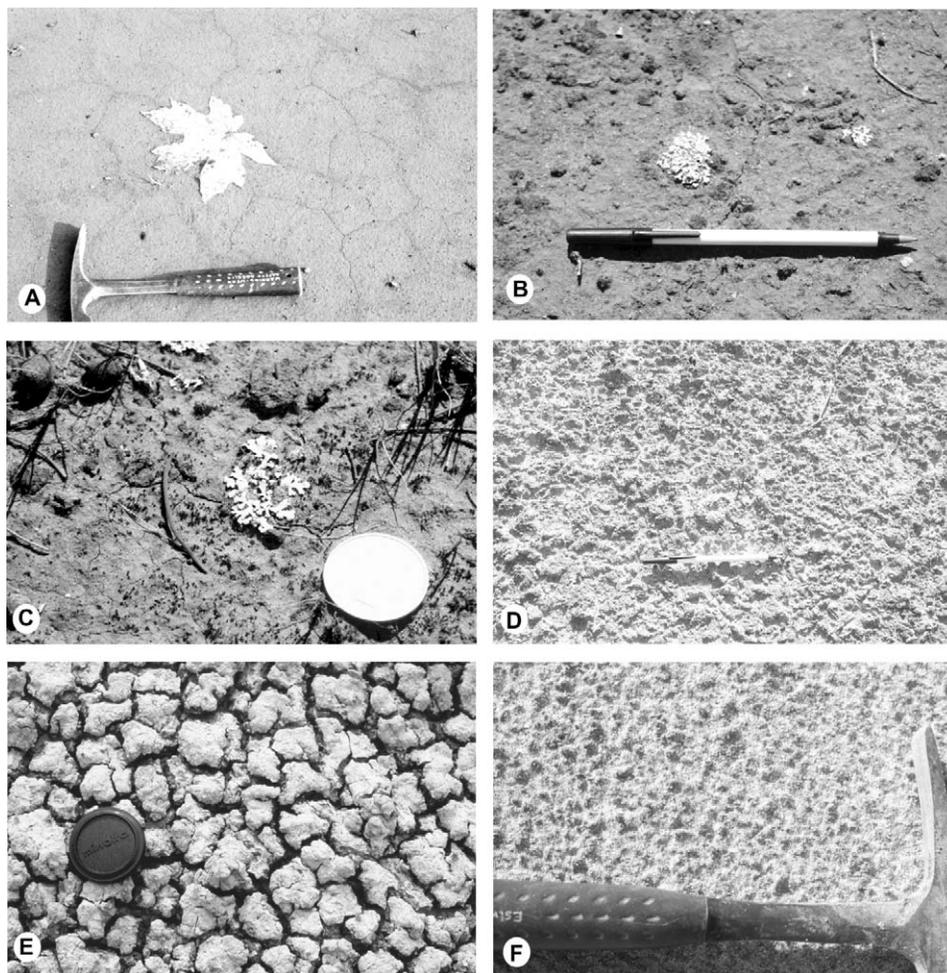


FIG. 3.—Modern surface textures of microbial earth: (A) transparent, cracked crust of cyanobacteria extending down into desiccation cracks, with leaf of big-leaf maple (*Acer macrophyllum*) from Dorena Lake, Oregon, USA (43.762618°N, 122.918619°W), (B) semitransparent, cracked crust with light-green foliose lichen (*Xanthoparmelia terrestris*), and fecal pellets on red soil between *Casuarina cristata* trees at Back Creek State Forest, 16 km east of West Wyalong, New South Wales, Australia (33.866138°S, 147.356428°E), (C) nontransparent, cracked, carpet texture crust, with light-green foliose lichen (*Xanthoparmelia reptans*), and fecal pellets on red soil between red mallee (*Eucalyptus socialis*) and porcupine grass (*Triodia scariosa*) near Damara station, New South Wales, Australia (34.154198°S, 143.329838°E), (D) nontransparent, cracked, “old elephant skin” crust with purple-gray lichens (*Psora decipiens*) between bluebush (*Maireana sedifolia*, *Maireana pyramidata*) and saltbush (*Atriplex nummularia*) at Lake Mungo National Park, New South Wales, Australia (33.730088°S, 143.044328°E), (E) deeply cracked (popcorn texture) smectite clay bound by desiccated interstitial lichens in badlands of Blue Mesa, Petrified Forest, Arizona, USA (34.943120°N, 109.772185°W), (F) gypsum crust with interstitial green cyanobacteria from Mormon Point, Death Valley National Park, California, USA (36.059020°N, 116.765351°W). Hammer for scale (A, F) is 25 cm long; pen (B, D) is 8 mm wide; coin (C) is 28.5 mm diameter; and lens cap (E) is 5.5 cm diameter.

near Karijini National Park, Western Australia (Fig. 4A–D; Simonson and Carney 1999, Pickard 2002); and in the Strelley Pool Formation (3430 Ma), at the Trendall locality south of North Pole Dome, Western Australia (Allwood et al. 2007). Memorable stromatolites were examined from the Beck Spring Dolomite (1300 Ma) near Tecopa, California (Licari 1978); the Helena Formation (1450 Ma) in Glacier National Park, Montana (Maliva 2001); and the Strelley Pool Chert (3430 Ma) at the Trendall locality near North Pole, Western Australia (Allwood et al. 2007).

Ancient examples of microbial earths and lichen polsterlands were discovered in the following units during a recent program of research on pre-Devonian paleosols: Devonian–Ordovician (400–450 Ma)

Grampians Group, Grampians National Park, Victoria, Australia (Retallack 2009b); Cambrian–Silurian (430–490 Ma) Tumblagooda Sandstone in Kalbarri National Park, Western Australia (Retallack 2009a); Early Ordovician–Cryogenian (480–630 Ma) Grindstone Range, Pantapinna, Balcoracana, Moodlatana, Billy Creek, Parachilna, Rawnsley, Bonney, and Nuccaleena formations in and around Flinders Ranges National Park, South Australia (Figs. 5A, B, E, 6A–C; Retallack 2008, 2009b); Stirling Range Quartzite (1800 Ma) on Barnett Peak, Stirling Range National Park, Western Australia (Fig. 5C, D; Bengtson et al. 2007); and Medicine Peak and Sugarloaf Quartzites (2500 Ma) near Medicine Peak, Wyoming (Kauffman and Steidtmann 1981, Kauffman et al. 2009).

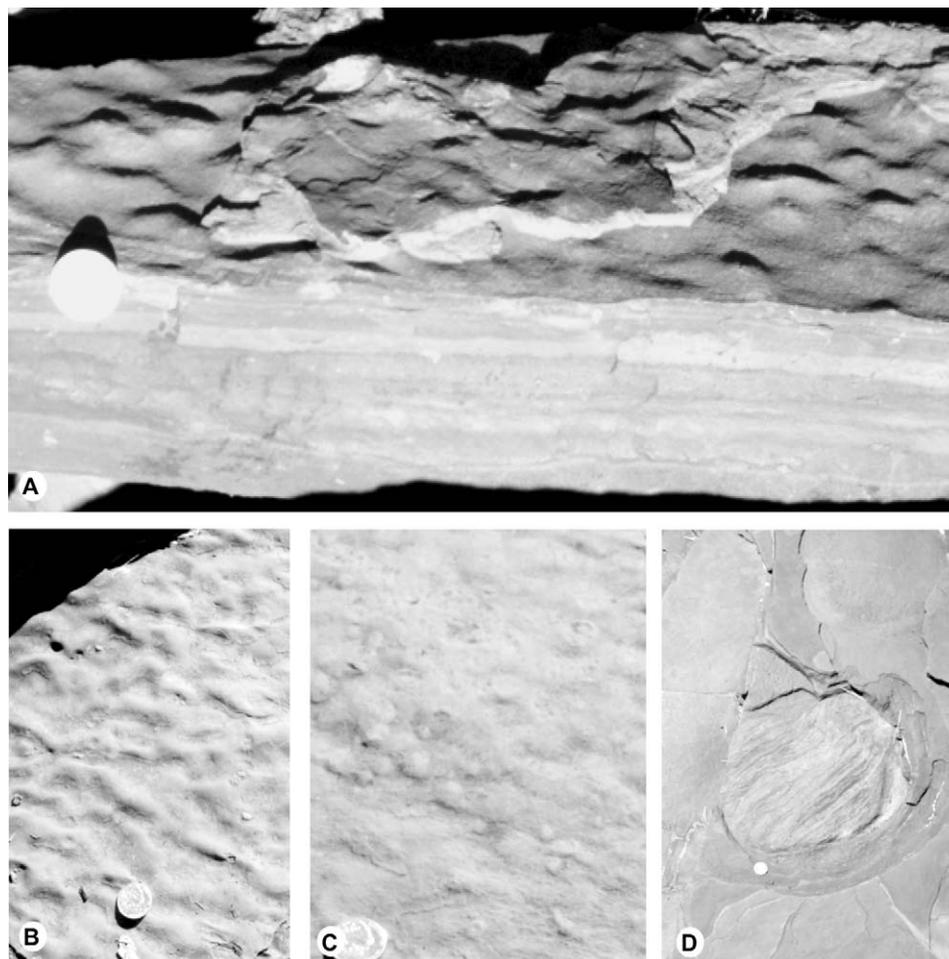


FIG. 4.—Fossil microbial mats: (A) tufted microbial mat surfaces (top) and layers from 2479 Ma, Mount McRae Shale, Mundjina Gorge, Western Australia (22.48789°S, 118.73144°E), (B–D) wrinkled (B), pustular (C), and redeposited flake (D) of microbial mats from the 2470 Ma Dales Gorge Member of the Brockman Iron Formation, near Kalamina Falls, Karajini National Park, Western Australia (22.41557°S, 119.40409°E). Australian 20c coin for scale in all images is 28.5 mm diameter.

MICROBIAL PRESERVATIONAL STYLES

Cellular permineralization in phosphate (Yuan et al. 2005), gold (Hallbauer and van Warmelo 1974, Hallbauer et al. 1977), calcite (Pflug 1994), or silica (Kenny and Krinsley 1992, 1998) has yielded the most convincing fossil record of Precambrian terrestrial lichens and microbes, but permineralization is rare in well-drained paleosols (Rye and Holland 2000). In Phanerozoic rocks, permineralized trees (Retallack 1981) and microbes (Klappa 1978, 1979; Trewin and Knoll 1999) are known from well-drained paleosols, but permineralization is more common in intertidal or wetland paleosols, such as Cambrian (510 Ma) phosphorites of Queensland (Fleming and Rigby 1972, Southgate 1986, Müller and Hinz 1992), the Devonian (410 Ma) Rhynie Chert of Scotland (Taylor et al. 2004), and (310 Ma) Pennsylvanian, calcite coal-balls of Illinois (Stubblefield and Taylor 1988). Most known Precambrian permineralized microbiotas are associated with marine or lacustrine stromatolites (Knoll et al. 1993, Schopf et al. 2007), banded iron formations (Maliva et al. 2005), or pillow basalts (Schopf and Packer 1987). Precambrian terrestrial microbiotas remain poorly known, and taxonomic differences between them and marine microbiotas are unclear.

Nodule preservation results from decay of buried organic matter, which in turn causes precipitation of a preservative cement (“authigenic cementation” of Schopf 1975), such as the siderite nodules surrounding weakly sclerotized Pennsylvanian animals and plants of Mazon Creek, Illinois (Shabica and Hay 1997), and fossil crabs from marine siderite nodules worldwide (Schweitzer and Feldmann 2000). Siderite and pyrite nodules are common in shallow-marine shales and in wetland paleosols, but they are unknown in well-drained paleosols (Retallack 1997a). Thin layers of ferric hydroxide cement coat leaves during their decay in aerated puddles (Spicer 1977), and observed in modern soils, this process explains the fine preservation of venation in fossil leaves of highly oxidized sandy paleosols (Retallack and Dilcher 1981). The comparable “pyritic death mask hypothesis” of Gehling (1999) infers that microbial decay early in Earth history induced pyritization capable of preserving megascopic fossils, a form of preservation unique to the Ediacaran period (540–635 Ma). The death mask model requires that the material now oxidized as red sandstones was once black and pyritic, but Ediacaran red beds are not due to post-Ediacaran oxidative weathering because they retain diagenetic calcite, illite, and chlorite, but no kaolinite, and they remain red beneath gray shales in boreholes (Goldring and Curnow 1967). My

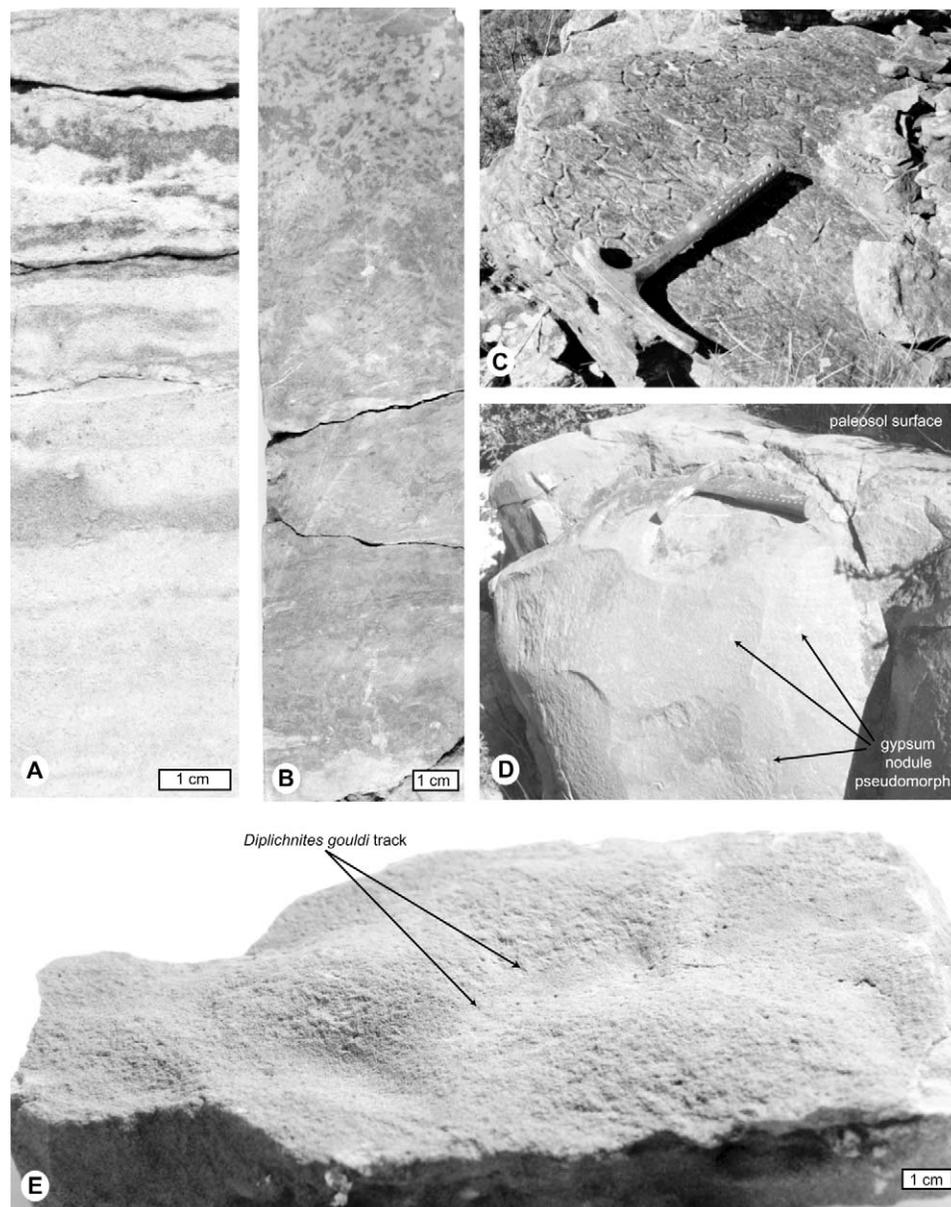


FIG. 5.—Fossil microbial earths: (A) polished slab of Upi pedotype paleosol with wide red burrows (*Myrowichmus arenaceus*) and narrow red strata of transgressive filaments from the Early Ordovician (ca. 484 Ma) Grindstone Range Sandstone in Ten Mile Creek, South Australia (31.25365°S, 138.97791°E), (B) polished slab of Mindi paleosol with narrow drab-haloed filaments from the Middle Cambrian (ca. 509 Ma) upper Moodlatana Formation in Ten Mile Creek, South Australia (31.25736°S, 138.94142°E), (C, D) desiccation-cracked sandstone (C) and paleosol profile (D) with subsurface nodules (Gypsid) in the 1.8 Ga Stirling Range Quartzite on Barnett Peak, Stirling Range, Western Australia (34.34874°S, 117.88250°E), and (E) oblique view of pustular microbial earth texture (*Rivularites repertus*) with smooth depressions that include an arthropod trail (*Diplichnites gouldi*) from a Wilpi pedotype paleosol (Psamment) in the Early Ordovician (ca. 484 Ma) Grindstone Range Sandstone in Ten Mile Creek, South Australia (31.25365°S, 138.97791°E).

own extensive thin section and microprobe work in South Australia (Retallack 2011) and comparable studies in correlative rocks of the Northern Territory (Mapstone and McIlroy 2006) have failed to demonstrate pyrite in association with Australian Ediacaran fossils, which owe their relief to structural chitin (Retallack 1994, 2007) and fine detail to Spicer's (1977) mechanism of ferric hydroxide encrustation. In contrast, Ediacaran fossils of the White Sea in Russia are encased in pyrite films and distinctive lumpy pyrite nodules that

overgrow and obscure their morphology (Dzik and Ivantsov 2002), in a way comparable with pyrite nodules of mangrove soils (Altschuler et al. 1983).

Drab-haloed root traces are another variety of authigenic alteration in which the chemical reduction of oxidized portions of paleosols by bacterial decay creates prominent green clayey mottles within the red matrix. In waterlogged paleosols, there is open-system translocation of iron and manganese, but little loss of iron is detectable when the drab

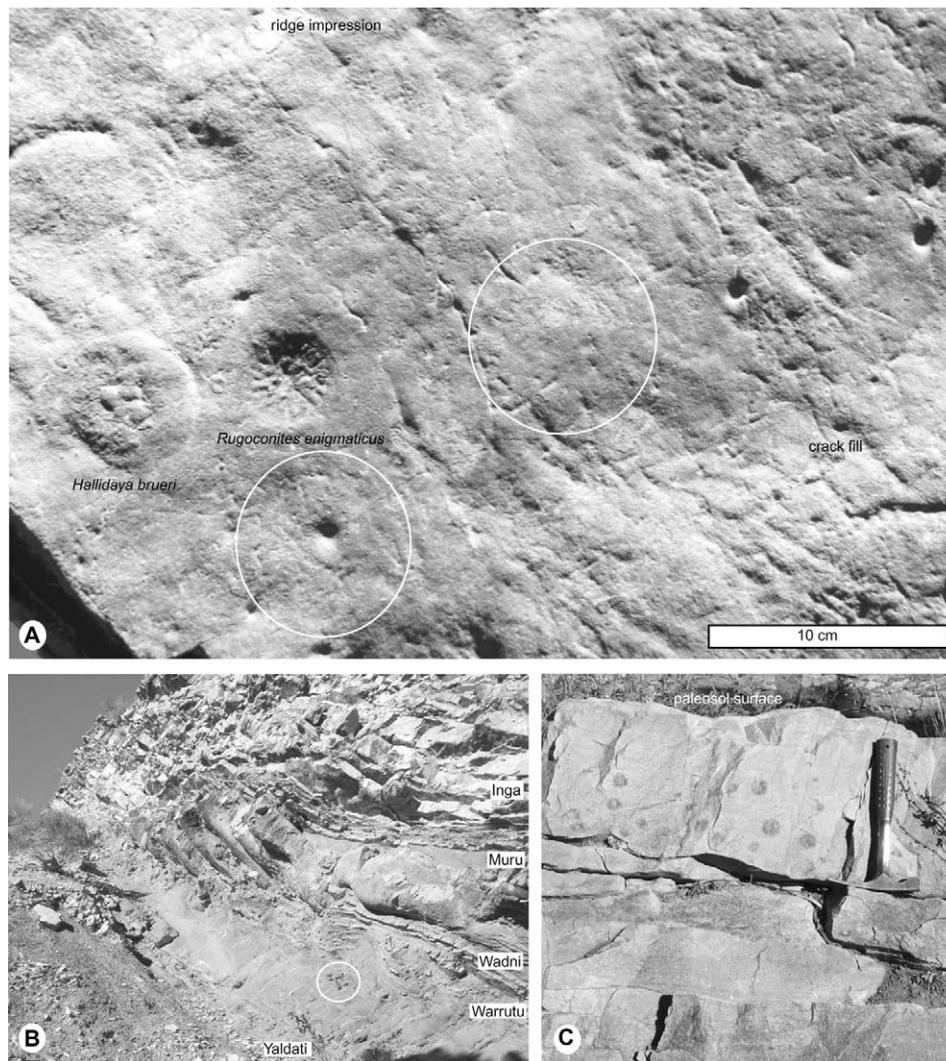


FIG. 6.—Microbial earths and paleosols of the late Ediacaran (ca. 555 Ma), Ediacara Member of the Rawnsley Quartzite, Flinders Ranges, South Australia: (A) *Rivularites repertus* (“old elephant skin”) showing sutured radial growth, crack fills, and ridge impressions, along with fossil impressions (*Hallidaya brueri* in positive relief, and *Rugoconites enigmaticus* in negative relief), on sole of sandstone slab from Parachilna Gorge (31.130831°S, 138.509844°E), (B) paleosols showing very weak (Wadni pedotype), weak (Yaldati pedotype), and moderate development (Muru, Warrutu, and Inga pedotypes) in Brachina Gorge, and (C) Inga pedotype paleosol with a distinct subsurface horizon of sand crystals pseudomorphous after gypsum, also in Brachina Gorge (31.34422°S, 138.55763°E). The fossiliferous surface (A) is part of a large slab on display in the South Australian Museum, Adelaide. The hammer for scale in B and C has a length of 25 cm.

haloes formed in well-drained paleosols sealed by burial (Retallack 1997b). Both kinds of filamentous green mottles are known in Precambrian red paleosols and are evidence of microbial earths of seasonally waterlogged soils in the 1800 Ma Lochness Formation near Mount Isa, Queensland (Driese et al. 1995) and of well-drained soils in the 550 Ma Ediacara Member of the Rawnsley Quartzite in Brachina Gorge, South Australia (Fig. 6B; Retallack 2011). The central tube of these drab-haloed fossils is larger than cyanobacterial filaments and was presumably formed around larger structures such as supracellular ropes (Garcia-Pichel and Wojciechowski 2009) or rhizines (Vogel 1955).

Biomineralization of seashells, corals, bones, and teeth has created most of the Phanerozoic fossil record, and when dissolved by groundwater or weathering, these fossils remain as molds and casts.

These complex skeletal hard parts are formed under direct cellular control, and they are examples of organic-matrix-mediated biomineralization. Stromatolites, on the other hand, are biomineralized by simple encrustation with calcite, dolomite, iron-manganese, or pyrite because of local chemical changes induced by metabolic pathways of the living microbial community (Grotzinger and Knoll 1999, Schieber 1999, Reid et al. 2000, Kazmierczak and Altermann 2002). Biologically induced ministromatolites of iron-manganese are common in rock varnish of modern deserts (Perry and Adams 1978, Krinsley 1998) and may be present in the 2200 Ma Waterval Onder paleosol near Waterval Onder, South Africa (Retallack 1986). Thecamoebans are living soil protists that have a vase-shaped organic-matrix-mediated exoskeleton, and a fossil record extending back $>742 \pm 6$ Ma in the Chuar Group of the Grand Canyon, Arizona

(Porter et al. 2003). This locality has been interpreted as shallow marine, not the usual soil habitat of thecamoebans, although the succession does include brecciated red beds (Dehler et al. 2005).

Compressions are the principal preservational form of organic unskeletonized fossils, and these leave impressions in shale and sandstone when the organic matter itself has been destroyed (Schopf 1975). Carbonaceous compressions are mostly preserved in gray to black shales, such as the 1030 Ma lower Neryuensk Formation (Lakhanda Series) in the Ust Maya region of Siberia, which include a variety of putative slime molds (*Mycosphaeroides aggregatus*, Myxomycota) and fungi (*Eosaccharomyces ramosus*, Ascomycota; *Mucorites ripheicus*, Zygomycota) of kinds best known today from soils (Hermann and Podkovryov 2006). Filamentous and spheroidal compressions are also common in Neoproterozoic intertidal shales (Schieber 1999, Callow and Brasier, 2009). Ellipsoidal carbonaceous compressions of uncertain origin also are known from the 2200 Ma Waterval Onder paleosol near Waterval Onder, South Africa (Retallack 1986, Retallack and Krinsley 1993).

Many Phanerozoic paleosols have impressions of leaf litter, roots, stumps, and footprints preserved by covering sandstones (Retallack and Dilcher 1981; Retallack 1997a, 2009a). Similar surface impressions of Precambrian paleosols could be a promising source of information about microbial earths of the past (Figs. 5C, D, 6A–C). These types of MISS (Noffke et al. 2001a, 2001b; Noffke 2008, 2009), OES (Bottjer and Hagadorn 2007), and TOS (Gehling and Droser 2009) are increasingly being recognized in Precambrian rocks, and distinguishing marine from nonmarine organic textures is the main purpose of this account. Similarly, endolithic microbial borings in the chilled margins of pillow basalts reveal marine microbial communities of the Precambrian (Furnes et al. 2008, McLoughlin et al. 2009). Unlike cellular permineralization or carbonaceous impressions though, such fossils offer little prospect of organic chemical or histological information about the fossils. Only general morphology is preserved in sandstone impressions (Fig. 6A).

PARATAXONOMIC APPROACHES TO FOSSIL MICROBES

Living microbes and lichens cannot easily be identified from their morphology alone: Chemical tests, and increasingly genome sequencing, are needed to identify them (Brodo et al. 2001). Thus, the existing taxonomy of Precambrian microbes is in effect a parataxonomic one, and it is accommodated within the concept of form genera of the International Code of Botanical Nomenclature (McNeill et al. 2006). Within such systems of uncertain taxonomic affinities, names that explicitly imply taxonomic affinities are to be avoided, although some unfortunate names remain valid. *Eomycetopsis* (Greek for dawn-fungus-like), for example, describes widespread permineralized tubes generally comparable with fungal hyphae, though they lack end walls and now are regarded as polysaccharide sheaths of mat-building cyanobacteria (Knoll 1982). *Tappania*, named for Helen Tappan, is an example of a taxonomically independent name, originally considered an acritarch (likely dinoflagellate resting cyst) but now regarded as an early multicellular fungal cyst (Dicaryomycota = Ascomycota + Basidiomycota; Butterfield 2005). Parataxonomies such as those for pollen (Traverse 2007) and stromatolites (Walter 1976) acknowledge uncertainty concerning taxonomic affinities.

Other microbial fossils are megascopic bedding plane textures, which can be labeled MISS (Noffke et al. 2001a, 2001b) or TOS, with common descriptive names such as “ropy,” “baggie,” or “elephant skin” (Gehling and Droser 2009), but they have also been given parataxonomic names. *Kinneyia similans*, for example, is a system of wrinkles with unusually steep sides and flat tops associated with carbonaceous filaments and laminae of microbial mats. Walcott (1914) established this name as a distinctive algal fossil from shaley partings

in the Mesoproterozoic (1300 Ma) Newland Formation of Montana (Schieber 1999), as a concept comparable with stromatolite form genera such as *Baicalia*, *Conophyton*, and *Thyssagites* (Walter 1976). Häntzschel (1975) regarded “*Kinneyia*” as miniature ripple marks, and thus a pseudofossil. Hagadorn and Bottjer (1997, 1999) also regarded “*Kinneyia*” as a pseudofossil (and stripped it of italicization) and as wrinkled microbial mats dissected by, and thus predating, soft-sediment burrows. Pflüger (1999) also demonstrated microbial mat affiliation of “*Kinneyia*” wrinkles but advocated wrinkling at the base (not top) of microbial mats under oscillating water levels of tidal flats. Whether it formed at the base or top of the mat, *Kinneyia* is considered here a valid form genus for a distinctive form of microbial mat created by particular fluid and biological conditions on tidal flats, generally comparable with stromatolites (Grotzinger and Knoll 1999). Like *Eocithrus*, which has a pustular rather than ridged morphology (Häntzschel 1975), *Kinneyia* is a useful parataxonomic name to express one form of sinuous to flexuous deformation of aquatic microbial mats.

A very different kind of sharp-edged, pustular-textured surface, with associated cracks and pedestals, is *Rivularites repertus*, described by Fliche (1906) along with fossil plants from Keuper (Late Triassic) fluvial facies of France. Fliche (1906) envisaged *Rivularites* as a distinctive microbial texture, and it is regarded here as a valid form genus for “elephant skin,” a textured organic surface best known from the Neoproterozoic Ediacara Member of the Rawnsley Quartzite of South Australia (Gehling and Droser 2009; fig. 3 is a superb example). My own field studies of “elephant skin” in the Ediacara Member have found it to be a natural mold at the base of covering sandstones over a variety of paleosol surfaces (Fig. 6). Similar fabrics have also been reported from Ordovician paleosols (Fig. 5E; Retallack 2009a). By this view, the name *Rivularites*, which implies a relationship with the living aquatic cyanobacterium *Rivularia*, is based on mistaken identity, comparable with *Eomycetopsis* and other valid but misleading names. Other indistinct fabrics from the Ediacara Member such as ropy-textured organic surfaces have been given the Latin binomial *Funisia dorothea* and have been compared with marine sponges or polyps (Droser and Gehling 2008). In my opinion, surfaces covered in *Funisia* more closely resemble puffballs, slime molds, or button lichens in modern soils (Figs. 1D, 3D). Such differences of opinion are the main reason for parataxonomic approaches to such fossils, and extend to other Ediacaran fossils, such as *Aspidella*, *Dickinsonia*, and *Ediacaria* (Retallack 1994, 2007, 2009a). The parataxonomic approach allows the rigor of type specimen definition and descriptions at a level of detail appropriate for fossil species of a wide variety of distinctive fossil forms, while acknowledging that their true systematic affinities are uncertain.

DIFFERENTIATING CRITERIA

The following paragraphs outline distinctions between microbial mats and microbial earths based largely on experience with both modern (Figs. 1–3) and fossil examples, but with emphasis on features preserved in fossil examples (Figs. 4–6). The following paragraphs depict extremes in the spectrum of variation from fully submerged aquatic microbial mats to well-drained microbial earths. These criteria can be confusingly combined in transitional environments such as tidal flats and lake margins, or in fluctuating environments, such as desert playas transiently awash after storms.

Textures and Relief

The most striking feature of modern aquatic microbial mats is their smooth to flexuous surface with fine striations oriented in the direction of flow (Figs. 1C, 2A). Modern microbial earths in contrast are lumpy to irregular, with numerous sharp bounding cracks or irregularly

sutured contacts from adjacent intergrown growth centers (Figs. 1B, 3D). Microbial earths form pedestals with shrunken buttresses and short narrow towers (Fig. 1B), but stromatolitic microbial mats have rounded domes or conical tufts (Fig. 1C). The internal fabric of this microrelief is also very different: vertical strands in microbial earths (Fig. 1B) and subhorizontal to domed lamination in stromatolitic microbial mats (Fig. 1C). Stromatolitic laminae show marked variation in porosity (Reid et al. 2000) not seen in microbial earths (Belnap 2003).

Color is a distinct feature in modern microbial mats, which are green to pink (Noffke 2010), whereas microbial earths are only transiently green and are more often multicolored, with flashes of orange and white on a general background of brown to black (Belnap 2003). Color is not preserved in the fossil record of microbial mats.

Desiccation cracks are found associated with both microbial mats and microbial earths because of changing tides and floods. Microbial mats either smooth over preexisting desiccation cracks or disruption by plant growth (Fig. 2B) or dry to a hard skin that is resistant to cracking (Fig. 2A). Microbial earths include desiccation cracks in sandy desert soils with little clay content (Fig. 1D). The binding effect of microbes thus induces loose sand to crack like clay (Prave 2002). Microbial earths of supratidal flats also show multiple generations of desiccation cracking, followed by microbial healing over and then cracking again, giving banded cracks or oscillation cracks (Noffke et al. 2006), a phenomenon conceptually similar to that which forms vertic soils (Paton 1974). In badlands slopes of expanding clays (smectites), a very complex system of cracks and irregularly swollen claystone clods (popcorn peds of Fig. 3E) is formed by the binding action of cyanobacteria and lichens (Finlayson et al. 1987, Cantón et al. 2004, Lazaro et al. 2008). Popcorn peds are near-equant angular clasts of clay quite distinct from the platy clasts produced by curling and erosion of microbial-mat-bound desiccation polygons, but these peds are water soluble (Finlayson et al. 1987) and require exceptionally high sedimentation rates or dry deposition to be preserved in the fossil record (Retallack 2005a). Desiccation cracks are formed by shrinkage of matrix as it dries, and they commonly (though not universally) have a deep V-shaped cross section (Weinberger 2001). "Syneresis cracks" are another form of shrinkage crack characterized by shallow, disconnected, sinuous tears, and they are U-shaped or irregular in cross section (Ehlers and Chan 1999, Pflüger 1999, Bouougri and Porada 2002). Syneresis in colloid chemistry is fluid expulsion from gels, but "syneresis cracks" have usually been attributed to subaqueous flocculation of clay due to salinity change or intrastatal fluidization during earthquakes (Pratt 1998). Comparable shallow sinuous cracks have been documented in modern and buried microbial mats of the intertidal zone of Tunisia by Noffke et al. (2001b), but they were attributed to transient desiccation of a gel-like mat rather than salinity-induced flocculation or earthquake.

Substrate Relationship

Modern microbial mats are nonadhesive to their mineral substrates, whereas modern microbial earths are intimately mixed with abundant mineral grains. Microbial mats include few silicate grains and may have abundant newly formed minerals such as calcite, especially in stromatolites (Reid et al. 2000) and "sand mats" (Pierson et al. 1987), but there is a clear demarcation between the base of the laminated to crinkly organic mat or stromatolite and grains of underlying sediment (Walter 1976, Hagadorn and Bottjer 1999, Schieber 1999). In microbial earths, however, cyanobacteria and other organisms take refuge from desiccation and hard radiation within a matrix of silicate grains, often to depths of many meters (Belnap 2003). The distance of tens of centimeters between densely colonized uppermost layers of the soil and underlying sparsely populated soil horizons is transitional.

These differences are most pronounced where microbial mats and

earths are eroded or disturbed by wildlife or humans. Microbial mats are redeposited as sheets, foldovers, and rollups (Schieber 1999, Simonson and Carney 1999, Noffke 2010), whereas microbial earths fall apart as individual organisms redeposited singly (Lazaro et al. 2008). This is especially clear at the edges of microbial mats, which are stepped down to the substrate (Fig. 1C), whereas the edges of microbial earths show a gradational profile of diminished erosion resistance from the organically bound surface to the less organic granular subsurface (Fig. 1B). The profile of dissected microbial mats is a vertical wall, perhaps with skeins of frayed filaments (Schieber 1999, Noffke et al. 2001a), whereas eroded microbial earths show a sinuous erosional profile, often overhanging because of the greater binding effect of organisms near the surface than in the subsurface (Belnap et al. 2003).

Subsurface Alteration

Modern microbial mats accrete like sedimentary layers above preexisting layers, which remain saturated and unbioturbated, and so preserve clear primary sedimentary structures. Cemented layers of living stromatolites, once considered subsurface diagenetic features, are now known to be formed at the surface (Reid et al. 2000). Microbial earths on the other hand are the uppermost part of soil profiles, which develop a variety of subsurface bioturbation and weathering features, often at the expense of sedimentary structures. For example, desiccation cracks covered by microbial mats after flooding of a dry playa are passively filled with layered organic matter or clay. In contrast, desiccation cracks within microbial earths show multiple episodes of cracking and sealing with wetting and drying, as reflected in layered clay skins (argillans) or zoned weathering rinds (sesquans in soil terminology; Retallack 1997a, 2001). Chemical alteration beneath microbial mats may include cementation with salts and chemical reduction, but chemical alteration beneath microbial earths is more or less marked by hydrolysis (incongruent solution of aluminosilicates to produce clay and cations). These processes can be revealed by chemical analyses and calculation of molar proportions of common cations (Ca, Mg, K, and Na), which are depleted compared with refractory elements (Al, Ti, Zr) in soils but stable or enriched in sediments (Retallack 1986, 2008, 2011; Beraldi-Campesi et al. 2009). Microbial earths of desert regions also are cemented by salts, including gypsum and calcite, but these form replacive nodules, with circumgranular cracks and micritic fabrics (Retallack 2005b, Retallack and Huang 2010), distinct from displacive salt crystals of euhedral forms found in supratidal and playa microbial mats (Pflüger 1999). Pedogenic carbonate of microbial earths is also fractionated from biologically respired soil carbon dioxide and so has a light carbon isotopic value ($\delta^{13}\text{C}$ of carbonate $< -2\%$ vs. Peedee belemnite [PDB]), whereas marine carbonate is isotopically heavier ($\delta^{13}\text{C}$ of carbonate $> -2\%$ vs. PDB; Sheldon and Tabor 2009).

Growth Series

Much of the variation within microbial mats and earths can be attributed to the different time for development of these communities, which reveal distinct modes of growth. Modern microbial earths develop like soils to a characteristic attenuation depth of biological activity adjusted to the supply of light, water, and nutrients available (Finlayson et al. 1987, Belnap 2003). Microbial earth organisms, like pioneering grasses of woodland ecosystems, are at first patchy and sparse, with minimal modification of preexisting sedimentary structures (Fig. 3A, B; transparent MISS of Noffke et al. 2001a), but then they thicken and fill in intervening spaces to completely rework the substrate to a characteristic depth, obscuring or destroying preexisting sedimentary structures (Fig. 3C, D; nontransparent MISS). Microbial mats can also appear transparent when first initiated and thin, but they continue to build upward in laminated layers through

TABLE 1.—Comparison of microbial mats and microbial earths.

Microbial mats	Microbial earths
Also known as pond scum, periphyton, algal lamination, biofilm, stromatolite	Also known as biological soil crust, cryptogamic earth, “old elephant skin”
Modern: Otematata, New Zealand; Black Rock Desert, Nevada; Everglades, Florida	Modern: Balranald, New South Wales, Australia; Canyonlands National Park, Utah; Kalbarri, Western Australia
Ancient: Fisher Formation (30 Ma), Oregon; Brockman Iron Formation (2470 Ma), Western Australia; Strelley Pool Formation (3350 Ma), Western Australia	Ancient: Tumblagooda Sandstone (460 Ma), Western Australia; Grindstone Range (484 Ma) and Rawnsley (555 Ma) Formations, South Australia; Stirling Range Formation (1900 Ma), Western Australia
Parataxonomic names: Kinneyia, Eoclathrus, etc.	Parataxonomic names: <i>Rivularites</i> , <i>Neantia</i> , etc.
Nonadhesive to substrate	Intimately mixed with substrate
Redeposited as sheets and rollups	Individual organisms redeposited singly
No hydrolytic weathering of substrate	Hydrolytic weathering of substrate
Abrupt mineral-texture contrast with substrate	Gradational mineral-texture contrast with substrate
Substrate cracks passively filled or absent	Substrate cracks with clayskins or oxidized (cutans)
$\delta^{13}\text{C}$ of carbonate $>-2\%$	$\delta^{13}\text{C}$ of carbonate $<-2\%$
Salt crystals or nodules displacive	Salt crystals or nodules replacive
Stromatolitic and tufted when thick	Subdued relief and unlayered when thick
Smoothing over desiccation cracks	Enabling desiccation cracks in sand
Syneresis cracks (deep U-section)	Desiccation cracks (deep V-section)
Domed or tufted growth centers	Peripherally sutured growth centers
Mounded and dimpled with expansion	Pressure ridges with expansion
Accretionary laminar growth	Characteristic profile development
Associated with ostracods, molluscs, marsh plants, mangroves	Associated with desert shrubs, lichen polsters
Lake or marine gray shale or limestone facies	Pyritic intertidal, red bed, or calcrete facies
Associated current ripples, rills, normal grading	Associated wind-dissected ripples, climbing translantent wind ripples
Aquatic-marine, submerged when alive	Intertidal, perilacustrine, soil

time, propagating basal irregularities or developing new domed or tufted irregularities in the case of stromatolites (Grotzinger and Knoll 1999, Schieber 1999, Noffke 2010).

Associated Organisms

Neither microbial mats nor microbial earths form such expansive areas today that all other organisms are excluded. The turquoise saline waters of Hamelin Pool stromatolites in Western Australia (Fig. 2C, D) are visited by few sea snakes, fish, and small marine snails and clams compared with Ningaloo coral reefs of the nearby open Indian Ocean. Microbial mats are excluded from most wave-protected seashores and lake margins by grazing of herbivorous mollusks and growth of seaweeds, glassworts, mangroves, salt marsh, and spike grass (Fig. 2B). A critical environmental variable fueling such biological competition is nutrient levels: Western Australian stromatolites are found with varied associated organisms and in varied salinities and temperatures, but always in oligotrophic waters (McNamara 1992).

Similarly, true microbial earths are limited in their distribution by widespread lichens, mosses, lycopsids, and desert shrubs, which may appear desiccated and dead, but which revive rapidly after rain (Rosentreter et al. 2008). Within dry woodlands, microbial earths on mineral soil between trees support common subterranean button lichens, but delicate large surface lichens are only found in sparsely grazed areas (Fig. 3B, C). In mesic woodlands and rain forest, a litter of bark and leaves, or ground cover of grass or spring ephemerals excludes most taxa of microbial earths (Belnap et al. 2003). In alpine and polar regions, microbial earths are limited by paucity of soil, with comparable lichens and cyanobacteria forming microbial rocklands,

often endolithic (Retallack 1992). Like microbial mats, microbial earths currently are found with other creatures capable of withstanding shortages of water, nutrients, and warmth.

Environmental Setting

Modern microbial mats are best known from aquatic sedimentary environments such as floodplains, lakes, and oceans (Noffke 2010). Microbial earths, like other soil communities of well-drained land, form during episodes of nondeposition, in both terrestrial sedimentary environments and on the kinds of erosional landscapes that will become major geological unconformities in the rock record (Belnap 2003). Thus, geological context can be important to their recognition in the fossil record. Microbial mats are to be expected in gray sandy, shaley, or calcareous marine, or pyritic intertidal facies (Boggs 1987, Schieber 1999), whereas microbial earths are found in evaporitic supratidal or playa, fluvial, red bed, or calcrete facies (Retallack 1997a, 2008, 2011). Sedimentary structures expected in association with microbial mats include current ripples, rills, and normally graded beds (Potter and Pettijohn 1963). Sedimentary structures expected in association with microbial earths are wind-dissected current ripples (“setulfs” of Hocking 1991), climbing-translantent wind ripples (Hunter 1977), and polygonal desiccation cracks (Weinberger 2001).

CONCLUSIONS

Limits to productivity of modern biological soil crusts in deserts include lack of water, heat, and essential nutrients, but soil crusts may have thrived also in warm-wet regions until displaced by more recently

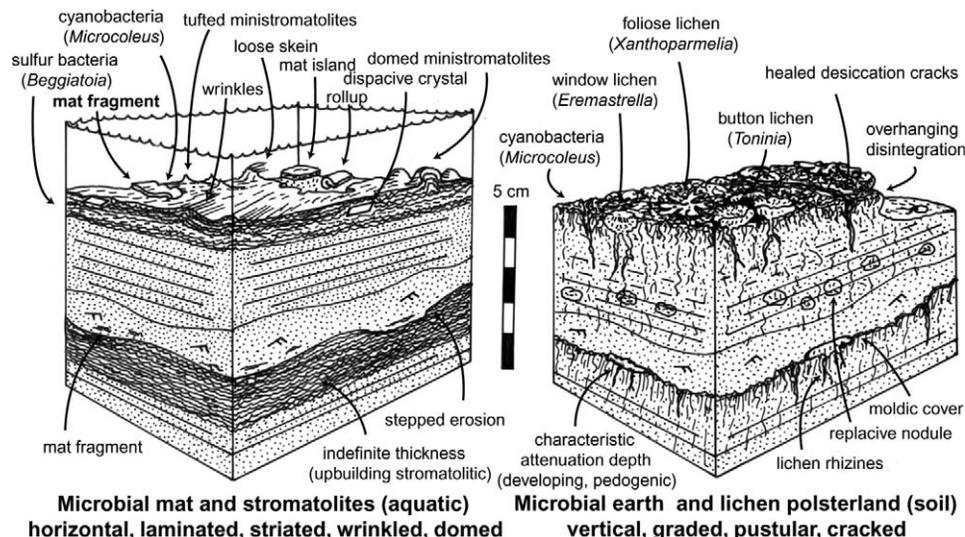


FIG. 7.—Cartoon comparison of modern microbial earths and mats.

evolved plant communities (Belnap et al. 2003), such as liverwort polsterlands dating back to the Middle Cambrian (510 Ma; Strother et al. 2004; Retallack 2008, 2009b), rhyniophyte brakelands dating back to the Early Silurian or latest Ordovician (440–450 Ma; Nohr-Hansen and Koppelhus 1988, Beck and Strother 2008, Retallack 2008, Tomescu et al. 2009), and progymnosperm woodlands dating back to the Middle Devonian (390 Ma; Retallack and Huang 2011). Lichen polsterlands with large lichens comparable to those in dry woodlands today (Fig. 3C) may have been widespread during the Ediacaran (635 Ma; Retallack 1994, 2007, 2011). Lichen polsterlands with small lichens comparable with modern biological soil crusts of deserts (Figs. 1D, 3D) may extend well back into the Archean (2760 Ma; Hallbauer and van Warmelo 1974, Hallbauer et al. 1977, MacRae 1999, Kositcin and Krapež 2004, Minter 2006, Mossman et al. 2008). Microbial earths extend back to 2760 Ma in the Mount Roe paleosol of the Hamersley Group near Whim Creek, Western Australia (Rye and Holland 2000). Tantalizing possible evidence of older microbial earths comes from microborings within pyrite grains in sandstones that include redeposited blocks of the immediately overlying pre-Strelley paleosol, Pilbara region of Western Australia (3430 Ma; van Kranendonk et al. 2006, Wacey et al. 2008, Wacey 2009). Such evidence needs to be sought also in the paleosol itself. The antiquity of microbial mats is comparable, from stromatolites in the 3430 Ma Strelley Pool Formation (Allwood et al. 2007) and permineralized microfossils in the 3458 Ma Apex Chert, both in the Pilbara region of Western Australia (Schopf and Packer 1987, Schopf et al. 2007, despite qualms about variation in preservation quality by Brasier et al. 2002).

The record outlined here is tantalizing and scarce because it is dependent on rare permineralizations and compressions, many of which were first discovered in the 1970s, when a deliberate worldwide search was made for black chert in sedimentary rocks. Such records of Precambrian life can be supplemented for other times and preservational environments by TOS (Gehling and Droser 2009), MISS (Noffke et al. 2006), and sedimentary petrography (Schieber 1999, Heubeck 2010). This paper seeks to expand the record of microbial ecosystems to clastic sedimentary environments on land by outlining a variety of criteria for distinguishing aquatic microbial mats from microbial earths (Table 1; Fig. 7). Such records of microbial earths and polster lands promise to be much more voluminous than records from permineralization and compression. The study of modern biological soil crusts

(Figs. 1, 3) and some ancient examples (Figs. 5, 6) will now provide new search images for additional evidence of early life on land.

ACKNOWLEDGMENTS

Mike Bilbo and Andy Baker aided with plant identification in the Black Rock Desert, Nevada, during the Burning Man Festival of 2008. Barbara and Warren Fargher graciously allowed access to Wirrealpa Station. Permission for research in nearby Flinders Ranges National Park was approved by Kate Wood, Ken Anderson, Darren Crawford, Arthur Coulthard, and Pauline Coulthard. Permission for research in Kalbarri National Park was approved by Kieran McNamara, Mike Paxman, and Russell Asplin. Examination of cores was aided by Brian Logan and Michael Willison at the Primary Industries and Resources South Australia Core Library in Glenside, Avi Olchina and Ken Sherring at the Geoscience Victoria Core Library in Werribee, and Chris Brooks at the Geological Survey of Western Australia Core Library in Carlisle. Ian Johnson, Diane Retallack, Christine Metzger, and Lisa Emerson helped with fieldwork. Arthur Mory, Ken McNamara, John Stolz, Richard Castenholz, Nora Noffke, Paul Strother, and Nathan Sheldon provided helpful discussion. This study was funded by American Chemical Society PRF grant 45257-AC8.

REFERENCES

- Aitken J. 1967. Classification and environmental significance of cryptalgal limestones and dolomites, with illustrations from the Cambrian and Ordovician of southwestern Alberta. *Journal of Sedimentary Petrology* 37:1163–1173.
- Allwood AC, Walter MR, Burch IW, Kamber BS. 2007. 3.43 billion year old stromatolite reef from the Pilbara Craton of Western Australia; ecosystem scale insights to early life on Earth. *Precambrian Research* 158:198–227.
- Altermann W. 2004. Precambrian stromatolites: problems in definition, classification, morphology and stratigraphy. In Eriksson PG, Altermann W, Mueller W, Catuneanu O (Editors). *The Precambrian Earth: Tempos and Events*: Elsevier, Amsterdam. p. 564–574.
- Altschuler ZS, Schnepfe MM, Silber CC, Simon FO. 1983. Sulfur diagenesis in Everglades peat and the origin of pyrite in coal. *Science* 221:221–227.
- Beck JH, Strother PK. 2008. Miospores and cryptospores from the Silurian section at Allenport, Pennsylvania, USA. *Journal of Paleontology* 82:857–883.
- Beeunas MA, Knauth LP. 1985. Preserved stable isotope signature of subaerial

- diagenesis in the 1.2 b.y. Mescal Limestone, central Arizona: implications for the timing and development of a terrestrial plant cover. *Geological Society of America Bulletin* 96:737–745.
- Belnap J. 2003. Comparative structure of physical and biological soil crusts. In Belnap J, Lange OL (Editors). *Biological Soil Crusts: Structure, Function and Management*: Springer, Berlin. p. 177–191.
- Belnap J, Büdel B, Lange OL. 2003. Biological soil crusts: characteristics and distribution. In Belnap J, Lange OL (Editors). *Biological Soil Crusts: Structure, Function and Management*: Springer, Berlin. p. 3–55.
- Belnap J, Harper KT. 1995. Influence of cryptobiotic soil crusts on elemental content of tissue of two desert seed plants. *Arid Land Research and Management* 9:107–115.
- Bengtson S, Rasmussen B, Krapež B. 2007. The Paleoproterozoic megascopic Stirling biota. *Paleobiology* 33:351–381.
- Beraldi-Campesi H, Hartnett HE, Anbar A, Gordon GW, Garcia-Pichel F. 2009. Effect of biological soil crusts on soil elemental concentrations: implications for biogeochemistry and as traceable biosignatures of ancient life on land. *Geobiology* 7:348–359.
- Boggs S. 1987. *Principles of Sedimentology and Stratigraphy*: Merrill, Columbus. 784 p.
- Bottjer D, Hagadorn JW. 2007. Mat features in sandstones: mat growth features. In Schieber J, Bose P, Eriksson PG, Banerjee S, Sarkar S, Altermann W, Catuneanu O (Editors). *Atlas of Microbial Mat Features Preserved within the Siliciclastic Rock Record*: Elsevier, Amsterdam. p. 53–71.
- Bouougri E, Porada H. 2002. Mat-related sedimentary structures in Neoproterozoic peritidal passive margin deposits of the West African craton (Anti-Atlas, Morocco). *Sedimentary Geology* 153:85–106.
- Brasier MD, Green OR, Jephcoat AP, Klepeš AK, van Kranendonk MJ, Lindsay JF, Steele A, Grassineau NV. 2002. Questioning the evidence for Earth's oldest fossils. *Nature* 416:76–81.
- Bristol BM. 1919. On the retention of vitality by algae from old stored soils. *New Phytologist* 18:92–107.
- Brodo IM, Sharnoff SD, Sharnoff S. 2001. *Lichens of North America*: Yale University Press, New Haven. 795 p.
- Butterfield NJ. 2005. Probable Proterozoic fungi. *Paleobiology* 31:165–181.
- Callow RHT, Brasier MD. 2009. Remarkable preservation of microbial mats in Neoproterozoic siliciclastic settings: implications for Ediacaran taphonomic models. *Earth-Science Reviews* 96:207–219.
- Cantón Y, Solé-Benet A, Domingo F. 2004. Temporal and spatial patterns of soil moisture in semiarid badlands of SE Spain. *Journal of Hydrology* 285:199–214.
- Chazottes V, Cabioch G, Golubic S, Radtke G. 2009. Bathymetric zonation of modern microborers in dead coral substrates from New Caledonia; implications for paleodepth reconstructions in Holocene corals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 280:456–468.
- Condon D, Zhu M, Bowring S, Wang W, Yang A, Jin Y. 2005. U-Pb ages from the Neoproterozoic Doushantuo Formation, China. *Science* 308:95–98.
- Costerton JW. 2007. *The Biofilm Primer*: Springer, New York. 199 p.
- Dehler CM, Elrick M, Bloch JD, Crossey LJ, Karlstrom KE, Des Marais D. 2005. High-resolution $\delta^{13}\text{C}$ stratigraphy of the Chuar Group (ca. 770–742 Ma), Grand Canyon; implications for mid-Neoproterozoic climate change. *Geological Society of America Bulletin* 117:32–45.
- Dott RH. 2003. The importance of eolian abrasion in supermature quartz sandstones and the paradox of weathering on vegetation-free landscapes. *Journal of Geology* 111:387–405.
- Driese SG, Simpson E, Eriksson KA. 1995. Redoximorphic paleosols in alluvial and lacustrine deposits, 1.8 Ga Lochness Formation, Mt. Isa: pedogenic processes and implications for paleoclimate. *Journal of Sedimentary Research* A66:58–70.
- Droser ML, Gehling JG. 2008. Reproduction and synchronous aggregate growth in a new Ediacaran tubular organism. *Science* 319:1660–1662.
- Dzik J, Ivantsov AY. 2002. Internal anatomy of a new Precambrian dickinsoniid dipleurozoan from northern Russia. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 7:385–396.
- Ehlers TA, Chan MA. 1999. Tidal sedimentology and estuarine deposition of the Proterozoic Big Cottonwood Formation, Utah. *Journal of Sedimentary Research* 69:1169–1180.
- Eldridge DJ, Greene RSB. 1994. Microbiotic soil crusts—a review of their roles in soil and ecological processes in the rangelands of Australia. *Australian Journal of Soil Research* 32:389–415.
- Finlayson BL, Gerits J, van Wesemael B. 1987. Crusted microtopography on badlands slopes in southeast Spain. *Catena* 14:131–144.
- Fleming PJG, Rigby JK. 1972. Possible land plants from the Middle Cambrian, Queensland. *Nature* 238:266.
- Fliche P. 1906. Flore fossile du trias en Lorraine et en Franche-Comté. *Société des Sciences Nancy Séances* 6:1–66.
- Furnes H, McLoughlin N, Mühlenbachs K, Banerjee N, Staudigel H, Dilek Y, de Wit M, van Kranendonk M, Schiffman P. 2008. Oceanic pillow lavas and hyaloclastites as habitats for microbial life through time: a review. *Modern Approaches in Solid Earth Sciences* 4:1–68.
- García-Pichel F, Johnson SI, Youngkin D, Belnap J. 2003. Small scale vertical distribution of bacterial biomass and diversity in soil crusts from arid lands in the Colorado Plateau. *Microbial Ecology* 46:312–321.
- García-Pichel F, López-Cortés A, Nübel U. 2001. Phylogenetic and morphological diversity in soil desert crusts from the Colorado Plateau. *Applied and Environmental Microbiology* 67:1902–1910.
- García-Pichel F, Wojciechowski MF. 2009. The evolution of a capacity to build extra-cellular ropes enabled filamentous cyanobacteria to colonize highly erodible substrates. *PLoS ONE* 4:e7801.
- Gehling JG. 1999. Microbial mats in terminal Proterozoic siliciclastics; Ediacaran death masks. *Palaïos* 14:40–57.
- Gehling JG, Droser ML. 2009. Textured organic surfaces associated with the Ediacaran biota in South Australia. *Earth-Science Reviews* 96:196–206.
- Goldring R, Curnow CN. 1967. The stratigraphy and facies of the Late Precambrian at Ediacara, South Australia. *Geological Society of Australia Journal* 14:195–214.
- Golubic S, Hofmann H. 1976. Comparison of Holocene and mid-Precambrian Entophysalidaceae (Cyanophyta) in stromatolitic algal mats: cell division and degradation. *Journal of Paleontology* 50:1074–1082.
- Grotzinger JP, Knoll AH. 1999. Stromatolites in Precambrian carbonates: evolutionary mileposts or environmental dipsticks? *Annual Reviews Earth and Planetary Sciences* 27:313–358.
- Hagadorn JW, Bottjer DJ. 1997. Wrinkle structures; microbially mediated sedimentary structures common in subtidal siliciclastic settings at the Proterozoic–Phanerozoic transition. *Geology* 25:1047–1050.
- Hagadorn JW, Bottjer DJ. 1999. Reconstruction of a Late Neoproterozoic biotope: suspect-microbial structures and trace fossils at the Vendian–Cambrian transition. *Palaïos* 14:73–85.
- Hallbauer DK, Jahns HM, Beltmann HA. 1977. Morphological and anatomical observations on some Precambrian plants from the Witwatersrand, South Africa. *Geologische Rundschau* 66:477–491.
- Hallbauer DK, van Warmelo KT. 1974. Fossilized plants in thucolite from Precambrian rocks of the Witwatersrand, South Africa. *Precambrian Research* 1:193–212.
- Häntzschel W. 1975. *Treatise on Invertebrate Paleontology. Part. W: Miscellaneous. Supplement 1. Trace Fossils and Problematica*: Geological Society of America and University of Kansas Press, Boulder and Lawrence, 269 p.
- Hermann TN, Podkovryov VN. 2006. Fungal remains from the Late Riphean. *Paleontological Journal* 40:207–214.
- Heubeck C. 2010. An early ecosystem of Archean tidal microbial mats (Moodies Group, South Africa, ca. 32.Ga). *Geology* 17:931–934.
- Hocking RM. 1991. The Silurian Tumblagooda Sandstone, Western Australia. *Geological Survey of Western Australia Report* 27:1–125.
- Houseman DC, Powers HH, Collins AD, Belnap J. 2006. Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert. *Journal of Arid Environments* 66:620–634.
- Hu C-X, Liu Y-D, Song L-R, Zhang DL. 2002. Effect of desert soil algae on the stabilization of fine sands. *Journal of Applied Phycology* 14:281–292.
- Hunter RE. 1977. Basic types of stratification in small eolian dunes. *Sedimentology* 24:361–387.
- Kahle CFJ. 2007. Proposed origin of aragonite Bahaman and some Pleistocene marine ooids involving bacteria, nannobacteria(?), and biofilms. *Carbonates and Evaporates* 22:10–22.
- Kauffman EG, Elswick ER, Johnson CC, Chamberlain K. 2009. The first

- diversification of metazoan life: biogeochemistry and comparative morphology of 1.9–2.5 billion year old trace fossils to Phanerozoic counterparts. In 9th North American Paleontological Convention Proceedings: *Cincinnati Museum Center Scientific Contributions* 3:62.
- Kauffman EG, Steidtmann JR. 1981. Are these the oldest metazoan trace fossils? *Journal of Paleontology* 55:923–927.
- Kazmierczak J, Altermann W. 2002. Neoproterozoic biomineralization by benthic cyanobacteria. *Science* 298:2351.
- Kennedy M, Droser M, Mayer LM, Pevear D, Mrofka D. 2006. Late Precambrian oxygenation: inception of the clay mineral factory. *Science* 311:1446–1449.
- Kenny R, Krinsley DH. 1992. Silicified Mississippian paleosol microstructures; evidence for ancient microbial–soil associations. *Scanning Microscopy* 6:359–366.
- Kenny R, Krinsley DH. 1998. Silicified micropeloid structures from the 1.1 Ga Mescal Limestone, north-central Arizona; probable evidence for Precambrian terrestrial life. *Mountain Geologist* 35:45–53.
- Klappa CE. 1978. Biolithogenesis of *Microcodium*: elucidation. *Sedimentology* 25:489–522.
- Klappa CE. 1979. Lichen stromatolites: criterion for subaerial exposure and a mechanism for the formation of laminar calcretes (caliche). *Journal of Sedimentary Petrology* 49:387–400.
- Knauth LP, Kennedy MJ. 2009. The late Precambrian greening of the Earth. *Nature* 460:728–732.
- Knoll AH. 1982. Microfossils from the Late Precambrian Draken Conglomerate, Ny Friesland, Svalbard. *Journal of Paleontology* 56:755–790.
- Knoll AH, Fairchild IJ, Swett K. 1993. Calcified microbes in Neoproterozoic carbonates: implications for our understanding of the Proterozoic/Cambrian transition. *Palaaios* 8:512–525.
- Kositcin N, Krapež B. 2004. Relationship between detrital zircon age-spectra and the tectonic evolution of the late Archaean Witwatersrand Basin, South Africa. *Precambrian Research* 129:141–168.
- Krinsley DH. 1998. Models of rock varnish constrained by high resolution transmission electron microscopy. *Sedimentology* 45:711–725.
- Lazaro R, Cantón Y, Solé-Benet A, Bevan J, Alexander R, Sancho LG, Puigdefabregas J. 2008. The influence of competition between lichen colonization and erosion on the evolution of soil surfaces in the Tabernas badlands (SE Spain) and its landscape effects. *Geomorphology* 102:252–266.
- Licari GR. 1978. Biogeology of the pre-Phanerozoic Beck Spring Dolomite of eastern California. *Journal of Paleontology* 52:767–792.
- MacRae C. 1999. *Life Etched in Stone: Fossils of South Africa*: Geological Society of South Africa, Johannesburg. 305 p.
- Maliva RG. 2001. Silicification in the Belt Supergroup (Mesoproterozoic), Glacier National Park, Montana, USA. *Sedimentology* 48:887–896.
- Maliva RG, Knoll AH, Simonson BM. 2005. Secular change in the Precambrian silica cycle; insights from chert petrology. *Geological Society of America Bulletin* 117:835–845.
- Mapstone NB, McIlroy D. 2006. Ediacaran fossil preservation; taphonomy and diagenesis of a discoid biota from the Amadeus Basin, central Australia. *Precambrian Research* 149:126–148.
- McLoughlin N, Furnes H, Banerjee NR, Mühlenbachs K, Staudigel H. 2009. Ichnotaxonomy of microbial trace fossils in volcanic glass. *Journal of the Geological Society of London* 166:159–169.
- McNamara K. 1992. *Stromatolites*: Western Australian Museum, Perth. 28 p.
- McNeill J, Barrie FR, Burdet HM, Demoulin V, Hawksworth DL, Marhold K, Nicolson DH, Prado J, Silva PC, Skog JE, Wiersma JH, Turland NJ (Editors). 2006. *International Code of Botanical Nomenclature (Vienna Code) Adopted by the Seventeenth International Botanical Congress, Vienna*: Ganter, Königstein, Germany. 568 p.
- Minter WE. 2006. The sedimentary setting of Witwatersrand placer mineral deposits in an Archaean atmosphere. In Kesler SE, Ohmoto H (Editors). *Evolution of Early Earth's Atmosphere, Hydrosphere, and Biosphere: Constraints from Ore Deposits*: Geological Society of America, Boulder, Colorado. Memoir 198, p. 105–119.
- Monger HC, Daugherty LA, Lindemann WC, Lidell CM. 1991. Microbial precipitation of pedogenic calcite. *Geology* 19:997–1000.
- Mossman DJ, Farrow CEG. 1992. Palaeosol and ore-forming processes in the Elliot Lake District of Canada. In Schidlowski M, Golubic S, Kimberley MM, McKirdy DM, Trudinger PA (Editors). *Early Organic Evolution: Implications for Mineral and Energy Resources*: Springer, Berlin. p. 67–75.
- Mossman DJ, Minter WEL, Dutkiewicz A, Hallbauer DK, George SC, Hennigh Q, Reimer TO, Horscroft FD. 2008. The indigenous origin of Witwatersrand 'carbon'. *Precambrian Research* 164:173–186.
- Müller LJ, Hinz I. 1992. Cambrogeorginidae fam. nov., soft-integumented problematica from the Middle Cambrian of Australia. *Alcheringa* 16:333–335.
- Noffke N. 2008. A turbulent lifestyle; microbial mats on Earth's sandy beaches, today and 3 billion years ago. *GSA Today* 18:4–8.
- Noffke N. 2009. The criteria for the biogenicity of microbially induced sedimentary structures (MISS) in Archaean and younger, sandy deposits. *Earth-Science Reviews* 96:173–180.
- Noffke N. 2010. *Geomicrobiology: Microbial Mats in Sandy Deposits from the Archaean Era to Today*: Springer, Berlin. 194 p.
- Noffke N, Gerdes G, Klenke T, Krumbein WE. 2001a. Microbially induced sedimentary structures—a new category within the classification of primary sedimentary structures. *Journal of Sedimentary Research* 71:649–656.
- Noffke N, Gerdes G, Klenke T, Krumbein WE. 2001b. Microbially induced sedimentary structures indicating climatological, hydrological and depositional conditions within recent and Pleistocene coastal facies-zones (southern Tunisia). *Facies* 44:23–30.
- Noffke N, Hazen R, Eriksson K, Simpson E. 2006. A new window into early life: microbial mats in siliciclastic early Archaean tidal flats (3.2 Ga Moodies Group, South Africa). *Geology* 34:253–256.
- Nohr-Hansen H, Koppelhus E. 1988. Ordovician spores with trilete rays from Washington Land, North Greenland. *Review of Palaeobotany and Palynology* 56:305–311.
- Paton TR. 1974. Origin and terminology for gilgai in Australia. *Geoderma* 11:221–242.
- Perry RS, Adams JB. 1978. Desert varnish: evidence of cyclic deposition of manganese. *Nature* 276:488–491.
- Pflug HD. 1994. Role of size increase in Precambrian organismic evolution. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 193:245–286.
- Pfänger F. 1999. Matground structures and redox facies. *Palaaios* 14:25–39.
- Pickard AL. 2002. SHRIMP U-Pb zircon ages of tuffaceous mudrocks in the Brockman Iron Formation of the Hamersley Range, Western Australia. *Australian Journal of Earth Sciences* 49:491–507.
- Pierson B, Oesterle A, Murphy GL. 1987. Pigments, light penetration and photosynthetic activity in the multilayered microbial mats of Great Sippewissett salt-marsh, Massachusetts. *FEMS Microbiology Ecology* 45:365–376.
- Porter SM, Meisterfeld R, Knoll AH. 2003. Vase-shaped microfossils from the Neoproterozoic Chuar Group, Grand Canyon; a classification guided by modern testate amoebae. *Journal of Paleontology* 77:409–429.
- Potter PE, Pettijohn FJ. 1963. *Paleocurrents and Basin Analysis*: Springer, Berlin. 296 p.
- Prashnowsky AA, Schidlowski M. 1967. Investigation of a Precambrian thucolite. *Nature* 216:560–563.
- Pratt BR. 1998. Syneresis cracks: subaqueous shrinkage in argillaceous sediments caused by earthquake-induced dewatering. *Sedimentary Geology* 117:1–10.
- Prave AR. 2002. Life on land in the Proterozoic: evidence from the Torridonian rocks of northwest Scotland. *Geology* 30:811–814.
- Reid RP, Visscher PT, Decho AW, Stolz JF, Bebout BM, Dupraz C, Macintyre IG, Paerl HW, Pinckney JL, Prufert-Bebout L, Steppe TF, DesMarais DJ. 2000. The role of microbes in accretion, lamination and early lithification of modern marine stromatolites. *Nature* 406:989–992.
- Retallack GJ. 1981. Comment on "Reinterpretation of the depositional environment of the Yellowstone fossil forests." *Geology* 9:52–53.
- Retallack GJ. 1986. Reappraisal of a 2200 Ma-old paleosol from near Waterval Onder, South Africa. *Precambrian Research* 32:195–232.
- Retallack GJ. 1988. Field recognition of paleosols. In Reinhardt J, Sigleo WR (Editors). *Paleosols and Weathering through Geologic Time: Principles and Applications*: Geological Society of America, Boulder, Colorado. Special Paper 216, p. 1–20.
- Retallack GJ. 1990. *Soils of the Past*: Unwin Hyman, London. 520 p.

- Retallack GJ. 1992. What to call early plant formations on land. *Palaaios* 7:508–520.
- Retallack GJ. 1994. Were the Ediacaran fossils lichens? *Paleobiology* 20:523–544.
- Retallack GJ. 1997a. *A Colour Guide to Paleosols*: Wiley, Chichester. 346 p.
- Retallack GJ. 1997b. Palaeosols in the upper Narrabeen Group of New South Wales as evidence of Early Triassic palaeoenvironments without exact modern analogues. *Australian Journal of Earth Sciences* 44:185–201.
- Retallack GJ. 2001. *Scovenia* burrows from Ordovician palaeosols of the Juniata Formation in Pennsylvania. *Palaeontology* 44:209–235.
- Retallack GJ. 2005a. Earliest Triassic claystone breccias and soil erosion crisis. *Journal of Sedimentary Research* 75:663–679.
- Retallack GJ. 2005b. Pedogenic carbonate proxies for amount and seasonality of precipitation in paleosols. *Geology* 33:333–336.
- Retallack GJ. 2007. Growth, decay and burial compaction of *Dickinsonia*, an iconic Ediacaran fossil. *Alcheringa* 31:215–240.
- Retallack GJ. 2008. Cambrian paleosols and landscapes of South Australia. *Australian Journal of Earth Sciences* 55:1083–1106.
- Retallack GJ. 2009a. Cambrian–Ordovician non-marine fossils from South Australia. *Alcheringa* 33:355–391.
- Retallack GJ. 2009b. Early Paleozoic pedostratigraphy and global events in Australia. *Australian Journal of Earth Sciences* 56:569–584.
- Retallack GJ. 2011. Neoproterozoic glacial loess and limits to snowball Earth. *Geological Society of London Journal* 168:1–19.
- Retallack GJ, Dilcher DL. 1981. Early angiosperm reproduction: *Prisca reynoldsii* gen. et sp. nov. from mid-Cretaceous coastal deposits in Kansas, USA. *Palaeontographica* B179:103–137.
- Retallack GJ, Huang C-M. 2010. Depth to gypsic horizon as a proxy for paleoprecipitation in paleosols of sedimentary environments. *Geology* 38:403–406.
- Retallack GJ, Huang C-M. 2011. Ecology and evolution of Devonian trees in New York, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 299:110–128.
- Retallack GJ, Krinsley DH. 1993. Metamorphic alteration of a Precambrian (2.2Ga) paleosol from South Africa revealed by back-scatter imaging. *Precambrian Research* 63:27–41.
- Retallack GJ, Mindszenty A. 1994. Well preserved Late Precambrian paleosols from northwest Scotland. *Journal of Sedimentary Research* A64:264–281.
- Retallack GJ, Orr WN, Prothero DR, Duncan RA, Kester PR, Ambers CP. 2004. Eocene–Oligocene extinction and paleoclimatic change near Eugene, Oregon. *Geological Society of America Bulletin* 116:817–839.
- Reuter M, Piller WE, Harzhauser M, Kroh A, Berning B. 2009. A fossil Everglades-type marl prairie and its paleoenvironmental significance. *Palaaios* 24:747–755.
- Rosentreter R, Bowker M, Belnap J. 2008. *A Field Guide to Biological Soil Crusts of Western US Drylands: Common Lichens and Bryophytes*: US Government Printing Office, Denver. 104 p.
- Rye R, Holland HD. 2000. Life associated with a 2.76 Ga ephemeral pond? Evidence from the Mount Roe #2 paleosol. *Geology* 28:483–486.
- Santelli CM, Edgecomb VP, Bach W, Edwards KJ. 2009. The diversity and abundance of bacteria inhabiting seafloor lavas positively correlate with rock alteration. *Environmental Microbiology* 11:86–98.
- Schieber J. 1999. Microbial mats in terrigenous clastics: the challenge of identification in the rock record. *Palaaios* 14:1–12.
- Schopf JM. 1975. Modes of fossil preservation. *Review of Palaeobotany and Palynology* 20:27–53.
- Schopf JW, Kudryavtsev AB, Czaja AD, Tripathi AB. 2007. Evidence of Archean life; stromatolites and microfossils. *Precambrian Research* 158:141–155.
- Schopf JW, Packer BM. 1987. Early Archean (3.3-billion to 3.5-billion-year-old) microfossils from Warrawoona Group, Australia. *Science* 237:70–73.
- Schweitzer CE, Feldmann RM. 2000. New fossil portunids from Washington, USA, and Argentina, and re-evaluation of generic and family relationships within the Portunoidea Rafinesque 1815 (Decapoda, Brachyura). *Journal of Paleontology* 74:636–653.
- Shabica CW, Hay AA (Editors). 1997. *Richardson's Guide to the Fossil Fauna of Mazon Creek*: Northeastern Illinois University, Chicago. 308 p.
- Sheehan PM, Harris MT. 2004. Microbialite resurgence after the Late Ordovician extinction. *Nature* 430:75–78.
- Sheldon ND, Tabor NJ. 2009. Quantitative paleoenvironmental and paleoclimatic reconstruction using paleosols. *Earth-Science Reviews* 95:1–95.
- Simonson BM, Carney KE. 1999. Roll-up structures; evidence of in situ microbial mats in late Archean deep shelf environments. *Palaaios* 14:13–24.
- Simpson WS, Simpson EL, Wizevich MC, Malenda HF, Hilbert-Wolf HL, Tindall SE. 2010. A preserved Late Cretaceous biological soil crust in the capping sandstone member, Wahweap Formation, Grand Staircase–Escalante National Monument, Utah: paleoclimatic implications. *Sedimentary Geology* 230:139–145.
- Southgate PN. 1986. Cambrian phoscrete profiles, coated grains and microbial processes in phosphogenesis, Georgina Basin, Australia. *Journal of Sedimentary Petrology* 56:429–441.
- Spicer RA. 1977. The pre-depositional formation of some leaf impressions: *Palaeontology* 20:907–912.
- Strother PK, Wood GD, Taylor WA, Beck JH. 2004. Middle Cambrian cryptospores and the origin of land plants. In Laurie JR, Foster CB (Editors). *Palynological and Micropalaeontological Studies in Honour of Geoffrey Playford*: Association of Australasian Palaeontologists, Canberra, Australia. Memoir 29, p. 99–113.
- Stubblefield SP, Taylor TN. 1988. Recent advances in palaeomycology. *New Phytologist* 108:3–25.
- Takashima C, Kano A. 2008. Microbial processes forming daily lamination in a stromatolitic travertine. *Sedimentary Geology* 208:114–119.
- Taylor TN, Klavins SD, Krings M, Taylor EL, Kerp H, Hass H. 2004. Fungi from the Rhynie Chert; a view from the dark side. *Royal Society of Edinburgh Earth Sciences Transactions* 94:457–473.
- Tomescu AMF, Pratt LM, Rothwell GW, Strother PK, Nadon GC. 2009. Carbon isotopes support the presence of extensive land floras pre-dating the origin of vascular plants. *Palaeogeography, Palaeoclimatology, Palaeoecology* 283:46–59.
- Traverse A. 2007. *Paleopalynology*: Springer, New York. 813 p.
- Trewin NH, Knoll AH. 1999. Preservation of Devonian chemotrophic filamentous bacteria in calcite veins. *Palaaios* 14:288–294.
- Vahrenkamp VC, Rossinsky V, Knauth LP, Beeunas MA. 1987. Preserved isotopic signature of subaerial diagenesis in the Mescal Limestone, central Arizona: discussion and reply. *Geological Society of America Bulletin* 99:595–597.
- van Kranendonk MJ, Hickman AH, Smithies RH, Williams IR, Bagas L, Farrell TR. 2006. Revised lithostratigraphy of Archaean supracrustal and intrusive rocks in the northern Pilbara Craton, Western Australia. *Geological Survey of Western Australia Record* 15:1–55.
- Vogel S. 1955. Niedere “Fensterpflanzen”: in der südafrikanischen Wüste. *Beiträge Biologie Pflanzen* 31:45–135.
- Wacey D. 2009. *Early Life on Earth: A Practical Guide*: Springer, Dordrecht. 274 p.
- Wacey D, Kilburn MR, McLoughlin N, Parnell J, Stokes CA, Brasier MD. 2008. Use of NanoSIMS to investigate early life on Earth: ambient inclusion trails within a ca. 3400 Ma sandstone. *Geological Society of London Journal* 165:43–45.
- Walcott CD. 1914. Cambrian geology and paleontology. III(2). Pre-Cambrian algal flora. *Smithsonian Miscellaneous Collections* 64:77–156.
- Walter MR. 1976. *Stromatolites*: Elsevier, Amsterdam. 790 p.
- Watanabe Y, Martini JEJ, Ohmoto H. 2000. Geochemical evidence for terrestrial ecosystems 2.6 billion years ago. *Nature* 408:574–578.
- Watanabe Y, Stewart BW, Ohmoto H. 2004. Organic- and carbonate-rich soil formation approximately 2.6 billion years ago at Schagen, east Transvaal District, South Africa. *Geochimica et Cosmochimica Acta* 68:2129–2151.
- Weinberger R. 2001. Evolution of polygonal patterns in stratified mud during desiccation; the role of flaw distribution and layer boundaries. *Geological Society of America Bulletin* 113:20–31.
- Wright VP, Tucker ME. 1991. Biological activity and laminar calcretes. In Wright VP, Tucker ME (Editors). *Calcretes*: Blackwell, Oxford. p. 205–206.
- Yuan X-L, Xiao S-H, Taylor TN. 2005. Lichen-like symbiosis 600 million years ago. *Science* 308:1017–1020.