

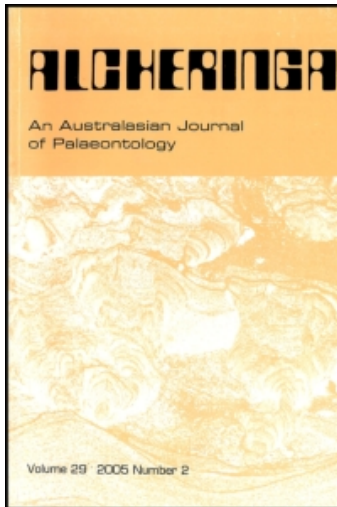
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Gregory J. Retallack^a

^a Department of Geological Sciences, University of Oregon, Eugene, OR, USA

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Cambrian–Ordovician non-marine fossils from South Australia

GREGORY J. RETALLACK

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Newly discovered trace and body fossils from the Grindstone Range Sandstone of South Australia reveal evidence of megascopic life on land during the Cambrian–Ordovician. Arthropod trackways (*Diplichnites gouldi*) are interpreted here to have formed on land. The most persuasive evidence for this view is that footprints vary in clarity along the length of the trackway as it traversed moist then dry silt, then biological soil crust. Compatible, though not diagnostic of walking on land is trackway symmetry, without one side buoyed up by current. The footprints bulge outward and are partially filled with miniature talus cones. Footprints also alternate as in walking, rather than opposite as in sculling. Arthropod resting traces (*Selenichnites* sp. indet.) have 11 lateral furrows, and footprints are bundled into sets of 8–11, most like euthycarcinoids. No arthropod dwelling burrows were found in associated palaeosols, so the track maker was more likely amphibious than fully terrestrial. Associated trace fossils include a new ichnotaxon of burrow, *Myrowichnus arenaceus* gen. et sp. nov. Thallose impressions (*Farghera robusta* gen. et sp. nov.) have the radiating dichotomous form of lichens, algae and liverworts. All these trace and body fossils were found in weakly developed palaeosols. Other palaeosols in the same formation are evidence of terrestrial ecosystems of modest biomass, weathering, carbon sequestration and stability in dry tropical regions.

Gregory J. Retallack [gregr@uoregon.edu], Department of Geological Sciences, University of Oregon, Eugene, OR 97403-1271, USA. Received 2.10.2008; revised 9.2.2009; accepted 5.3.2009.

Key words: Ordovician, South Australia, euthycarcinoid, track, trace fossil, lichen.

ANCIENT terrestrial ecosystems can now be studied using palaeosols, even in non-marine rocks as old as Ordovician and Cambrian (Retallack 2000, 2001, 2008). Insights from palaeosols into such ecosystem parameters as soil respiration and chemical weathering do not provide details of the organisms involved, because Cambrian and Ordovician palaeosols are sparsely fossiliferous, like geologically younger palaeosols (Retallack 1998). This article reports newly discovered assemblages of Cambrian–Ordovician non-marine trace and body fossils in palaeosols. The plant-like fossils are problematic but were more likely lichens or algae than plants. Trackways may reveal arthropod excursions onto

land, and burrows may reveal the limits of the soil water-table. Although biological affinities of this new assemblage are uncertain, they provide macroscopic images of a terrestrial ecosystem prior to Late Ordovician millipede-liverwort communities (Retallack 2001).

The main purpose of this work is a formal description of a newly discovered assemblage of trace and body fossils from the Grindstone Range Sandstone of South Australia. Sedimentary palaeoenvironments, palaeoclimate and palaeosols of this new biota have been described elsewhere (Stock 1974, Moore 1990, Retallack 2008, 2009). Palaeobiological and palaeoecological interpretations of such poorly preserved and largely unprecedented fossils are a challenge but are attempted here following systematic description.

Materials and methods

Exposures of the Grindstone Range Sandstone were examined in Ten Mile (N31.25364° E138.97793°) and Balcoracana creeks (S31.17246° E138.92963°) in the eastern Flinders Ranges, South Australia (Figs 1, 2). Stratigraphic sections were measured using the method of eyeheights. An environmental SEM was used (University of Oregon's FEI Quanta) to obtain high-resolution images without conductive coating.

Trace fossils and body fossils are named here with legal provisions of the International Code of Zoological Nomenclature

(Ride *et al.* 1999) for trace fossils and fossils of uncertain fungal-animal affiliation (Retallack 1994), and palaeobotanical provisions of the International Code of Botanical Nomenclature (McNeill *et al.* 2006) for morphogenera of problematic plant-like impressions. Toponomic nomenclature of trace fossils follows Martinsson (1970). All specimens (numbers prefixed P-) are held in the collections of the South Australian Museum, Adelaide. Specimens were collected from two palaeosols and intervening flaggy sandstone of the Grindstone Range Sandstone in Ten Mile and Balcoracana creeks, Wirrealpa Station, South Australia (Fig. 1). Measurements of cross-sectional

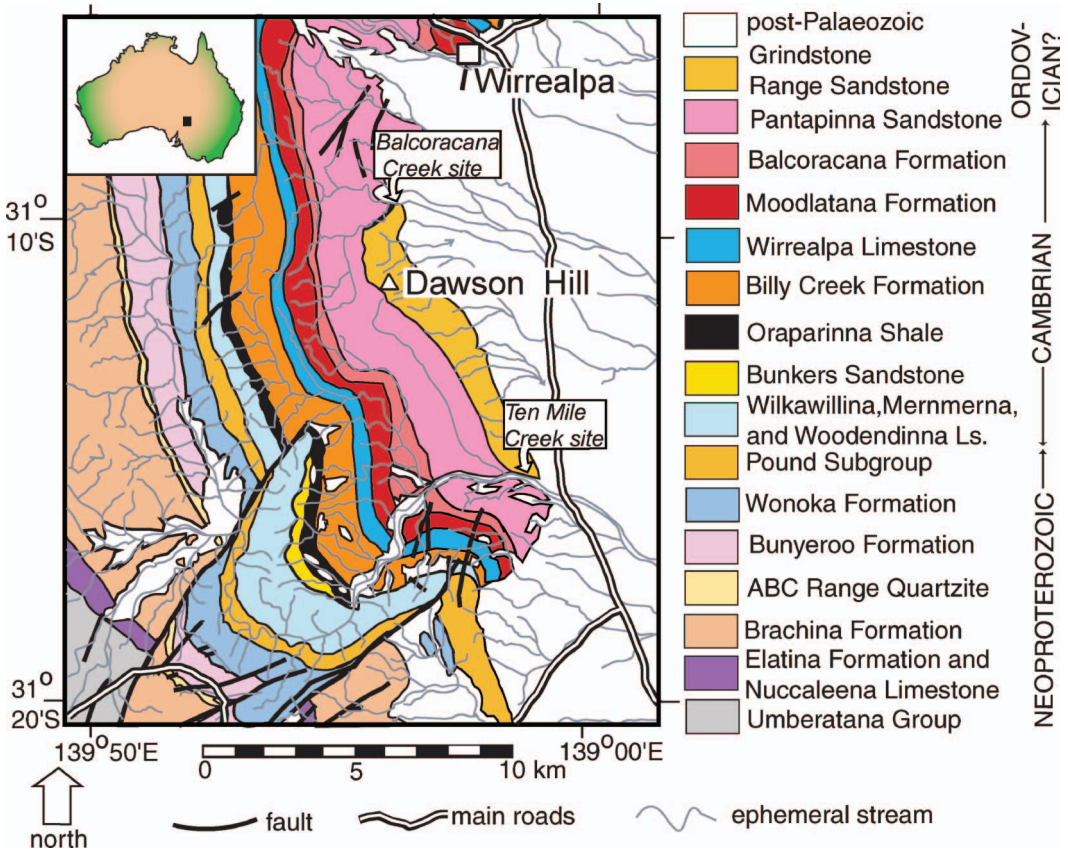


Fig. 1. Geological map and Early Ordovician fossil localities in the Grindstone Range Sandstone in Ten Mile and Balcoracana creeks, South Australia.

Sandstone is also no younger than Late Ordovician (Hirnantian, 446.3 ± 2.2 Ma), which is the oldest U–Pb isochron age of local granites and Delamerian deformation in the northern Flinders Ranges, much younger than Delamerian deformation further south in South Australia (Elburg *et al.* 2003).

The geological age of the Grindstone Range Sandstone is poorly constrained biostratigraphically and radiometrically, but two lithological correlation techniques favour an age of Early Ordovician (Tremadocian) suggested by Daily & Forbes (1969), rather than late Cambrian (Jago *et al.* 2006). First, linear extrapolation of tie points in the Ten Mile Creek section (Fig. 2A) dates the fossiliferous level of the Grindstone Range Sandstone as 483 Ma (± 2.8 Ma from standard error of correlation and dating), assuming near-constant long-term rate of sedimentation suggested by lack of marked changes in grain size (Retallack 2008). These tie points (diamonds in Fig. 2A) are as follows: (1) negative $\delta^{13}\text{C}_{\text{carb}}$ excursion at 1152 m correlated with one at 538 Ma in Siberia (by Tucker 1991, Kirschvink & Raub 2003); (2) $^{206}\text{Pb}/^{238}\text{U}$ SHRIMP zircon (SL13 standard) age of 522.8 ± 1.8 Ma for tuff at 2389 m (Haines & Flöttmann 1998, Gravestock & Shergold 2001); (3) first appearance of trilobite *Redlichia guizhouensis* at 3170 m correlated with the late Lungwangmaioan (511.5 Ma) *R. guizhouensis* Zone of China (Jago *et al.* 2006, Paterson & Brock 2007); (4) trilobite *Onaraspis rubra* at 3533 m (Jago *et al.* 2006), taken as coeval with the 509.5 Ma *Oryctocephalus indicus* Zone (Geyer & Shergold 2000, Gradstein *et al.* 2004); and (5) agnostid *Leiopyge laevigata* at 3882 m (Daily & Forbes 1969), dated internationally at 504 Ma (Gradstein *et al.* 2004).

Second, pedostratigraphic correlation of the deep-calcic palaeosol, representing a transient palaeoclimatic change, near the base of the Grindstone Range Sandstone

with comparable palaeosols in the Officer Basin of South Australia and northern Perth Basin of Western Australia also suggests a geological age slightly younger than the Cambrian–Ordovician boundary (Retallack 2009). The age of this deep-calcic palaeosol in the Officer Basin is constrained by underlying volcanics dated by K–Ar at 484 ± 4 Ma (Table Hill Volcanics of Stevens & Apak 1999) and 483.6 ± 20 Ma and 493.7 ± 20 Ma (Kulyong Volcanics of Major & Teluk 1967, corrected using the decay constants of Dalrymple 1979). The deep-calcic palaeosol in the Officer Basin also underlies the Indulkana Shale, which has been correlated with the Horn Valley Siltstone of the Amadeus Basin and its Castlemainian trilobite (*Lycophron freemani*) assemblage (Laurie 2006), equivalent to Llanvirnian of Avalonia and dated at *ca* 468 Ma (Gradstein *et al.* 2004).

Systematic palaeontology

Kingdom and Phylum INCERTAE SEDIS

Aspidella Billings, 1872

Aspidella terranovica Billings, 1872
(Figs 3B–F; 4B–C; 5D)

Description. These circular to elliptical structures protrude from bed tops, or are deeply recessed, as sandstone casts or moulds of a compaction-resistant body. They have strong relief, with a central depression and radiating grooves within an outer ridge. The South Australian specimens have a central depression 3 mm in diameter (mean with standard deviation ± 1.4 mm, for 30 specimens), whereas the mean outside diameter is 9.0 mm (± 3.0 mm for 39).

Comparisons. *Bergaueria*, *Beltanelliformis* (McIlroy *et al.* 2005) and *Conostichus* (Mángano *et al.* 1996) resemble some

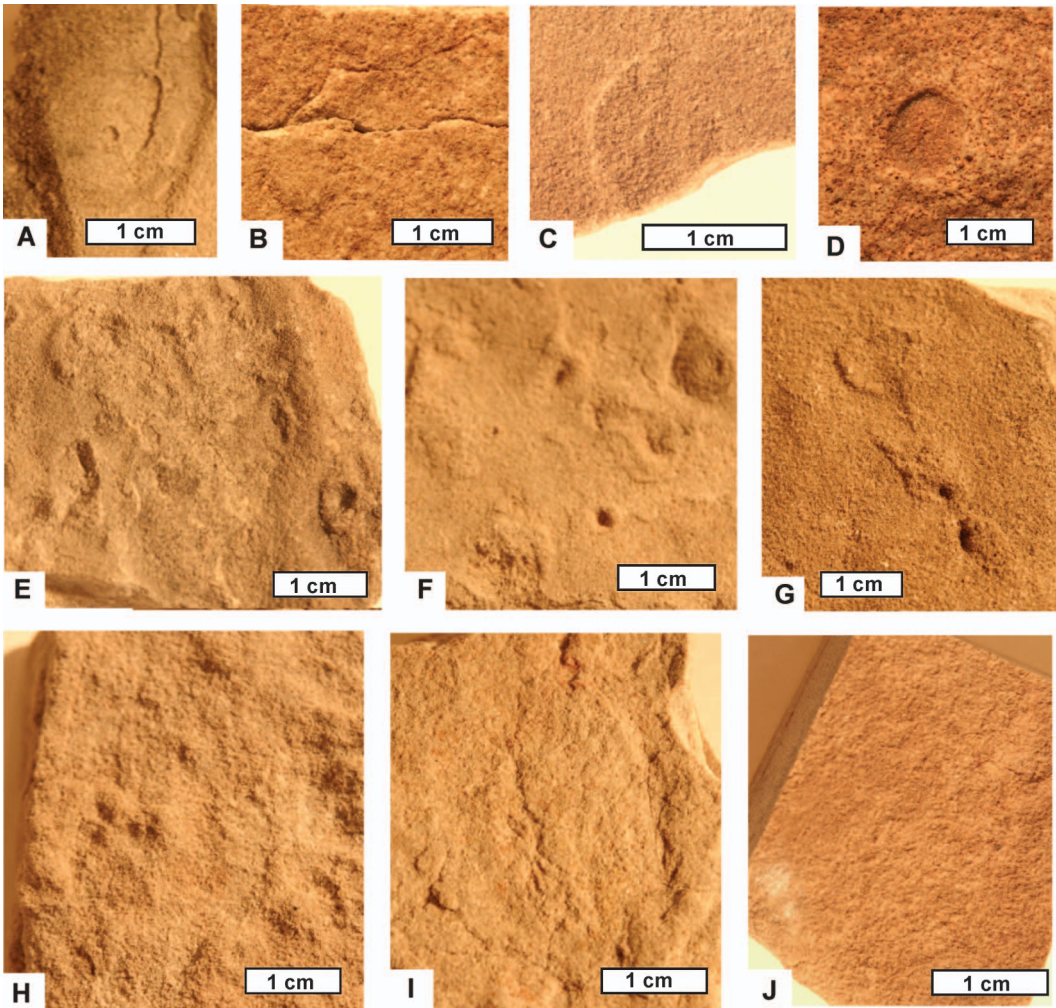


Fig. 3. Enigmatic (Ediacaran holdover?) body fossils from the tops of beds of the Grindstone Range Sandstone in Ten Mile Creek, South Australia: **A**, *Spriggia wadea* (P42299); **B–F**, *Aspidella terranovica* (P42284, P42330, P42347, P42301, P42303 respectively); **G–H**, *Ediacaria flindersi* (P42324, P42294 respectively); **I–J**, *Rutgersella* sp. (P42293, P42332 respectively).

morphs of *A. terranovica*, but lack regular radial grooves, or radially arranged tubular extensions. *Laevicyclus* (Seilacher 1955) is a superficially similar pit and mound structure, but lacks radial grooves and lateral folds. The South Australian fossils are similar to the type material of Billings (1872) in having high relief and radial grooves. At the type locality near Ferryland, Newfoundland, in the Ediacaran Fermeuse

Formation, *Aspidella terranovica* grades into forms with concentric and finely radiating grooves, similar to *Spriggia* and *Ediacaria*, which have been included within the *A. terranovica* complex by Gehling *et al.* (2000). These other taxa are separated here, and also found in the Grindstone Range Sandstone (Figs 3A, G–H; 4A, D–E). As in Newfoundland and other Ediacaran occurrences (Mapstone & McIlroy 2006),

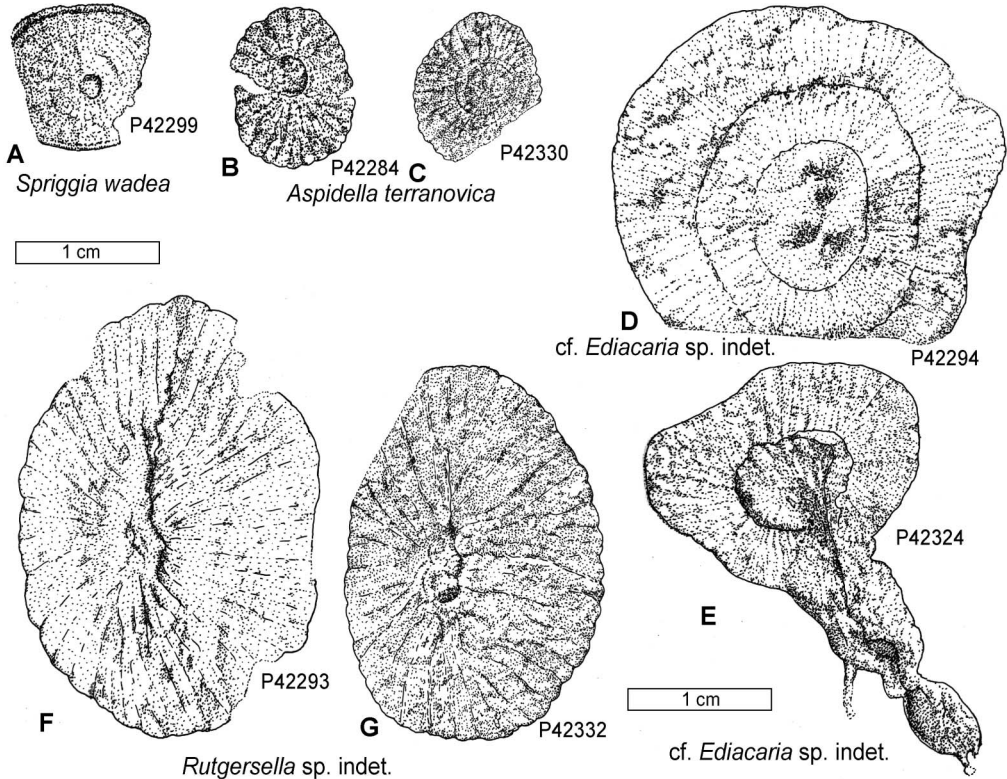


Fig. 4. Interpretative sketches of enigmatic (Ediacaran holdover?) fossils from the Grindstone Range Sandstone in Ten Mile Creek, South Australia.

Grindstone Range *Aspidella* is locally abundant and continues vertically through more than one bedding plane.

Affinities. *Aspidella terranovica* has been considered a cast of an anemone-like cnidarian body fossil (Gehling *et al.* 2000), but could also have been a bacterial colony (Steiner & Reitner 2001, Grazhdankin & Gerdes 2007) or fungal fruiting structure (Retallack 1994). *Aspidella* has also been considered a pseudofossil gas escape structure (Häntschel 1975), but shows folding, rims and radial grooves that resemble biological structures (Gehling *et al.* 2000). There is no trace of clay or organic matter in these fossils; they show only sand grains under the SEM (Fig. 5D). Radial extensions

outward and down into the sandstone (arrowed in Fig. 5D) are more like rhizines of lichens, hyphae of fungi or swarming streams of bacteria (Retallack 1994, Steiner & Reitner 2001), than tentacles of cnidarians (Gehling *et al.* 2000) or gas escape structures (Häntschel 1975).

Material. P42326, P42327, P42328, P42330, P42331, P42334, P42335, P42336 from Wilpi pedotype in Ten Mile Creek; P42299, P42300, P42301, P42302, P42303, P42347, P42349, P42350 from sediment in Ten Mile Creek.

Ediacaria Sprigg, 1947

cf. *Ediacaria* sp. indet. (Figs 3G–H; 4D–E)

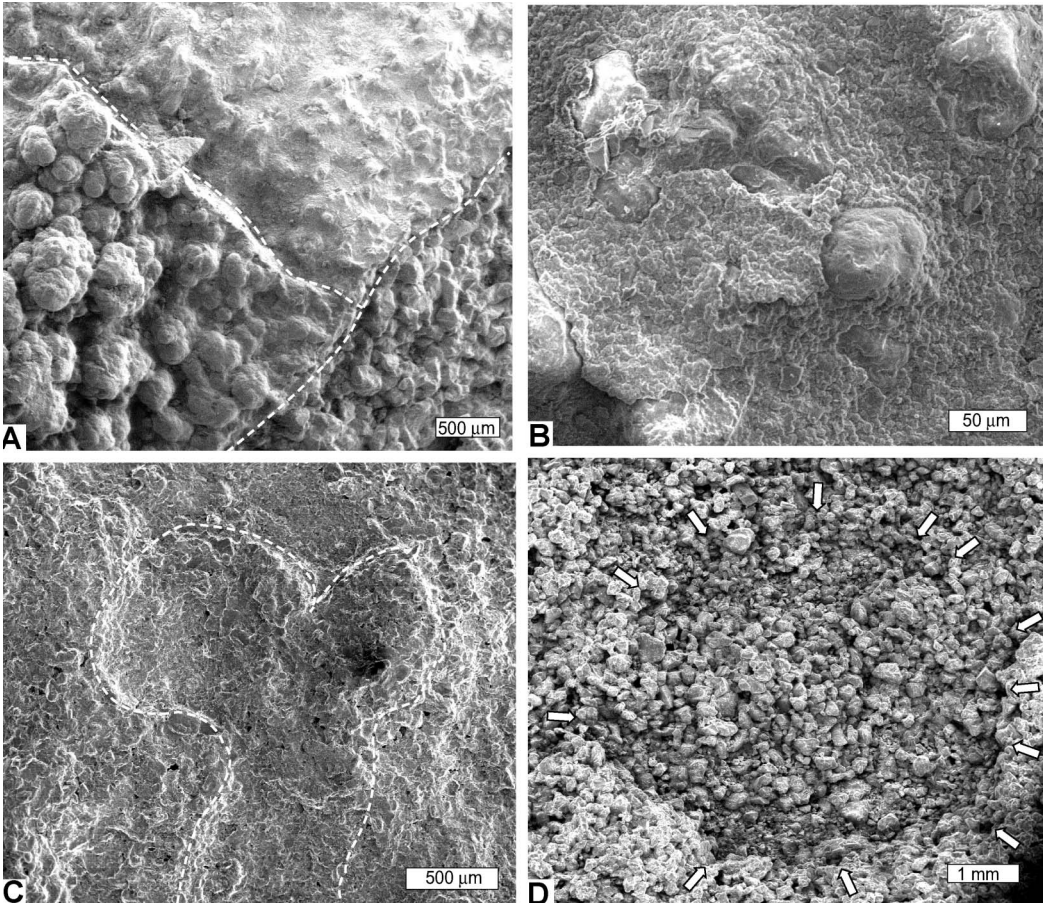


Fig. 5. Scanning electron micrographs of fossils from the Grindstone Range Sandstone in Ten Mile Creek, South Australia: **A–B**, branching axis *incertae sedis*. (P42290) showing three different surfaces: (1) botryoidal hematite coating (left in A), (2) grains of matrix (lower right in A) and (3) microtubular meshwork (upper left in A and all B); **C**, *Farghera robusta* sp. nov. (P42263a) showing dichotomizing thallus mould filled with clay and hematite compared with granular matrix; **D**, *Aspidella terranovica* (P42328) showing no trace of organic matter within sandstone matrix and radial fine filaments (at arrows) penetrating downward into sediment.

Description. These slightly convex, round, radially striated and concentrically lined body casts protrude from the tops of sandstone beds, in a manner comparable with associated *Aspidella*. Diameters average 26 mm (± 8.4 mm for 9), with a smooth interior circle of 11.4 mm (± 4.3 mm for 9). One faint impression from the Grindstone Range has attached elongate features, which appear pulled outward and upward to deform the overlying biomat (Figs 3G, 4E). Comparable elongate extensions were

also noted in specimens associated with large Ediacaran *Aspidella* (*sensu lato*) in Newfoundland (Gehling *et al.* 2000, text-fig. 14).

Comparison. *Ediacaria booleyi* is a form larger and more convex than the Grindstone Range fossils, from middle Cambrian rocks of Ireland (Crimes *et al.* 1995, Vanguetaine & Brueck 2005). Discoid fossils in sandstone from the Lower Ordovician Blaiklock Glacier Group, Antarctica

(Weber & Braddy 2004), and the late Cambrian Mount Simon-Wonewoc sandstones, Wisconsin (Hagadorn *et al.* 2002), are also larger and have a higher relief. *Ediacaria flindersi* is considered part of the *Aspidella terranova* complex in Ediacaran rocks (Gehling *et al.* 2000), but is distinct in its larger size yet finer ribbing than these comparable fossils in the Grindstone Range assemblage.

Affinities. *Ediacaria* has been considered a jellyfish or anemone (Sprigg 1947, Gehling *et al.* 2000), but could also be a bacterial colony (Steiner & Reitner 2001, Grazhdankin & Gerdes 2007), fungus or lichen (Retallack 1994). This debate is not settled by elongate structures associated with these fossils (Figs 3G, 4E; Gehling *et al.* 2000, text-fig 4), which could be a cnidarian stolon, lichen rhizines, or a mushroom stalk.

Material. P42355 from Upi pedotype in Ten Mile Creek; P42232, P42284, P42288, P42298, P42323, P42324, P42325, P42293, P42294 from Wilpi pedotype in Ten Mile Creek.

Farghera gen. nov. (Figs 6A–F; 7A–E)

Type species. *Farghera robusta* sp. nov.

Derivation of name: After Barbara Fargher of Wirrealpa Station.

Diagnosis. Thallus external moulds, branching dichotomously and monopodially outward from a central segment; ultimate thallus segments thin with rounded outline defined by thickened margins; thin tapering and branching threads attached to thallus margins, branching outward and downward.

Comparisons. *Farghera* is based on external moulds in sandstone filled with clay either red with hematite or yellow with goethite

(Retallack 2008). They are not pseudofossils, because these minerals and associated red clay are microcrystalline under SEM (Fig. 5C), and partially fill hollows in the rock with measurable thickness (Fig. 8G), unlike thin films of pyrolusite or other mineral dendrites or stains. Furthermore, most specimens of *Farghera* appear to be in growth position, because large slabs have evenly spaced and evenly sized individuals (Fig. 6E), and because their lateral threads arch outward and downward into the matrix (Fig. 6B) like roots or holdfasts. If the thalli were transported, their distribution would be more clumped and lateral threads would be in the same bedding plane and aligned by current. Preservation as oxidized moulds lacking organic matter renders biological affinities of *Farghera* uncertain, until discovery of more informative compressions or permineralizations.

Two commonly used palaeobotanical morphogenera for impressions of dichotomously branching thalli are *Thallites* Walton, 1923, and *Algites* Seward, 1894. *Thallites* is used for radially dichotomizing thalli similar to those of liverworts such as *Marchantia* (Smith 1990) and *Algites* for non-radial dichotomizing thalli comparable with those of algae, such as *Fucus* and *Dictyota* (Graham & Wilcox 2000). *Farghera* differs from both form genera because it has tapering threads orthogonal to the margins of the thallus (Figs 6B, 7A), similar to rhizines of foliose lichens such as *Parmelia* (Brodo *et al.* 2001) and holdfasts of algae such as *Caulerpa* (Graham & Wilcox 2000). Furthermore, not all branching of *Farghera* is dichotomous, because some branches are near-monopodial and irregular (Fig. 6G), as in lichens such as *Ramalina* (Brodo *et al.* 2001), and algae such as *Caulerpa* (Graham & Wilcox 2000).

Flabellitha Jurina & Krassilov, 2002, is a similar Devonian foliose ascolichen preserved as an organic compression with

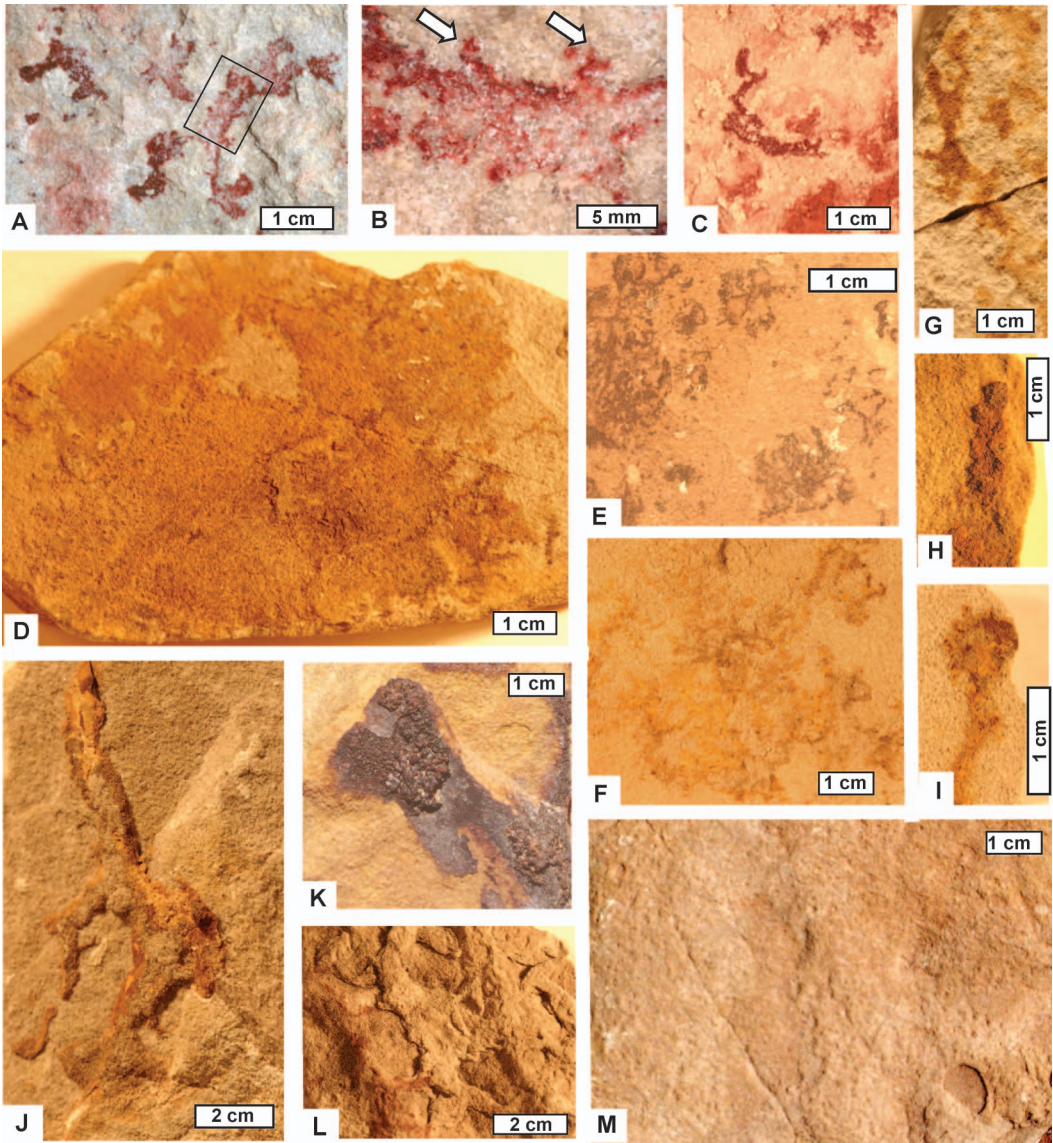


Fig. 6. Enigmatic fossils from the Grindstone Range Sandstone in Ten Mile and Balcoracana Creeks, South Australia: **A**, **C–G**, *Farghera robusta* sp. nov. (P42263a, P42264a, P42265, P42319, P42268, P42338, respectively), thallose external moulds; **B**, enlargement of area in rectangle of **A**; **H–I**, ovoid and circular structures *incertae sedis* (P42280, P42269, respectively); **J–K**, branching axes *incertae sedis* (P42322, P42290, respectively); **L–M**, *Rivularites repertus* (P42283, P42260, respectively), pustulose biological soil crust in sand bound by organisms so that desiccation cracks and bubbles formed like those in mudstone.

spores and cell outlines, so not merely a morphotaxon like *Farghera*. Dichotomies of *Flabellitha* are less divergent and the ultimate segments more wedge-shaped than in *Farghera*. *Flabellitha* also lacks the tapering

lateral threads of *Farghera*. *Spongiophyton* is preserved as thalloid organic compressions with microstructure and chemical composition suggestive of lichens (Chaloner *et al.* 1974, Gensel *et al.* 1991, Retallack

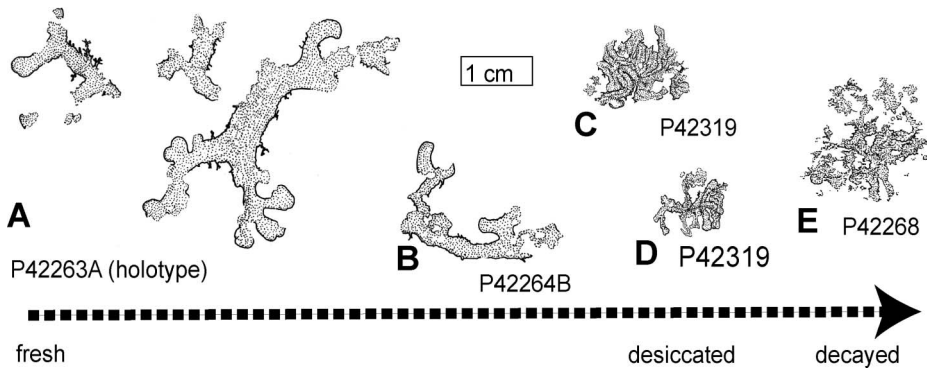


Fig. 7. Interpretative sketches of *Farghera robusta* sp. nov. from the Grindstone Range Sandstone in Ten Mile Creek, South Australia.

1994, Jahren *et al.* 2003, Taylor *et al.* 2004; but see also Fletcher *et al.* 2004). *Spongiophyton* shows neither the lateral threads nor dichotomies of *Farghera*. Other fossils with dichotomizing thalli and attached lateral threads are 'thalloid macrofossils' of Tomescu & Rothwell (2006), 'fossil impression' of Williams & Schmidt (2003), *Ichnuza cocozzi* (Debrenne & Naud 1981) and *Persimedesites chahgazensis* (Hahn & Pflug 1980). Collectively, these fossils are more compact or discoid than the most compact *Farghera* (Figs 6E, 7C–D).

Affinities. Dichotomizing flat thalli like *Farghera* are found in liverworts, algae and lichens. Neither liverworts nor algae have lateral tapering threads comparable with those of *Farghera*. Rhizoids of liverworts are smaller and parallel sided (Smith 1990). Lateral spines of algal thalli are shorter and algal holdfasts are not spread along the margins of laminae (Graham & Wilcox 2000). Neither algae nor liverworts have chitin or other biopolymers capable of maintaining almost 2 mm of thallus relief in deeply buried quartz sandstone (Retallack 2007, Brasier & Antcliff 2008). Nor are liverworts or algae found distributed through surface horizons of oxidized palaeosols (Retallack 2008).

The majority of living lichens of comparable thallose ground-dwelling form are ascolichens (*Heterodermea*, *Hypogymnea*, *Menegazzia*, *Parmelia*, *Parmelina*, *Parmeliopsis*, *Xanthoparmelia* of Brodo *et al.* 2001). The basidiolichen *Dictyonema glabratum* is also a ground-dwelling foliose lichen of broadly comparable form (Chaves *et al.* 2004: named in the Botanical Code by Agardh, 1821, before *Dictyonema* Hall, 1851, a graptolite genus in the Zoological Code). Basidiomycota may be as old as Devonian (Hueber 2001), and perhaps Late Ordovician (Arbey & Koeniguer 1979). Ascomycota, Chytridiomycota and lichenized Glomeromycota have a fossil record extending back to the Precambrian (Hallbauer & Van Warmelo 1974, Hallbauer *et al.* 1977, Retallack 1994, Butterfield 2005, Yuan *et al.* 2005). Spores, permineralized microstructures or geochemical biomarkers are needed to identify fossil lichens with modern fungal taxa, and none of these are likely to be preserved in the quartzites bearing *Farghera*.

***Farghera robusta* sp. nov.** (Figs 6A–F; 7A–E)

Holotype. P42263a from Upi palaeosol in ten Mile Creek.

Derivation of name. Latin *robustus* meaning strong, hardy.

Diagnosis. *Farghera* with stout (1–3 mm wide) thalli branching irregularly or dichotomously at intervals of 2–4 times thallus width, with rounded pairs of dichotomously branched terminal segments; marginal threads stout (1 mm wide) tapering and branching downward into matrix.

Description. Thalli average 1.4 mm wide (± 0.5 mm for 149), and the lateral threads average 0.5 mm diameter (± 0.1 mm for 11). There is no correlation between thallus width and thickness (Fig. 8G), which is evidence of a laminar spreading organism, with greater variation in thickness than expected for a compression fossil. Many specimens show isolated radial individuals

2–3 cm across (Figs 6E–F, 7C–D). One specimen is a clump of radially dichotomizing thalli with a diameter of 9 cm (Fig. 6D); perhaps an older individual or clonal clump.

Comparison. Grindstone Range Sandstone specimens of *Farghera* are considered monospecific because of the bell-shaped curve of 500 measured specimens (Fig. 8G–I). Variation in thickness, width and clumping of *Farghera* could be due to dehydration, quality of preservation, or stage of clonal growth (Fig. 7).

Material. P42263, P42264, P42265, P42266, P42267, P42268, P42269, P42270, P42271, P42272, P42274, P42275, P42273, P42297, P42319, P42320 from Upi pedotype on Ten Mile Creek; P42285, P42295 from Wilpi pedotype on Ten Mile Creek;

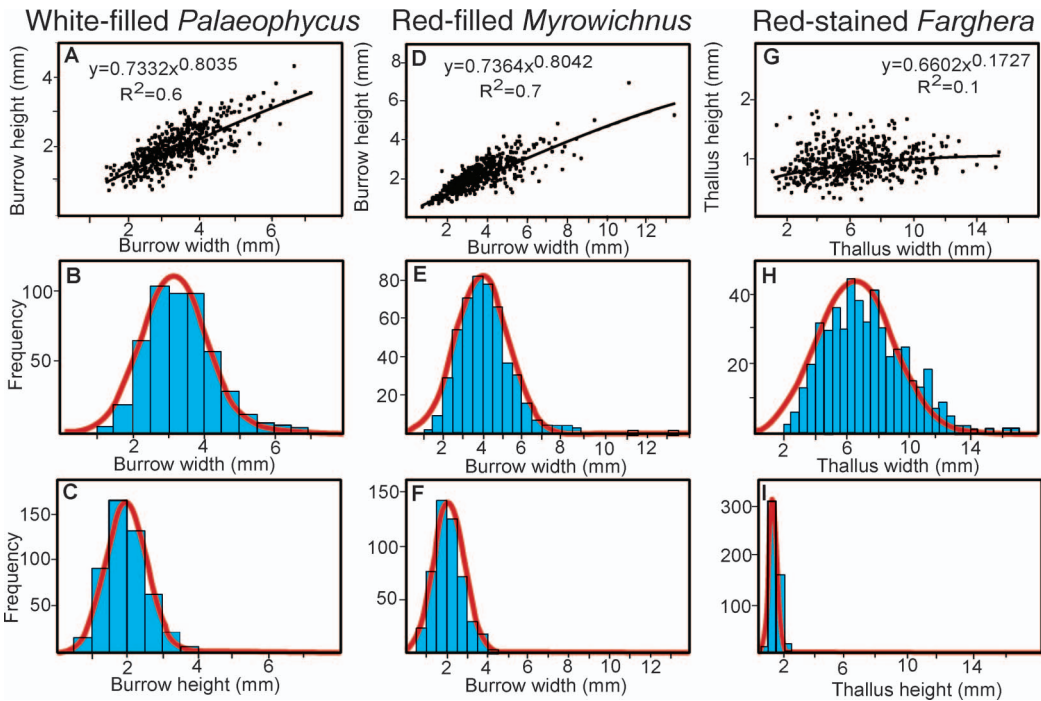


Fig. 8. Size distribution of fossils from the type Upi palaeosol in Ten Mile Creek, South Australia: A–C, *Palaeophycus heberti*, 500 measurements of burrows filled with white sandstone from cross-sections; D–F, *Myrowichnus arenaceus* gen. et sp. nov., 500 measurements of burrows with thick red siltstone walls and fill from cross-sections; G–H, *Farghera robusta* gen. et sp. nov., 500 measurements of dimensions of specimens exposed in cross-section. Heights are dimensions vertical to bedding, and widths are dimensions parallel to bedding.

P42237, P42338 from Upi pedotype on Balcoracana Creek.

Rutgersella Johnson & Fox, 1968

Rutgersella sp. indet. (Figs 3I–J; 4F–G)

Description. These faint elliptical external moulds with crude bilateral symmetry are depressions in the surface of sandstone slabs. Lateral ribs curve outward from an ellipsoidal depression, which plunges to one side as if slightly overfolded. Their mean length is 36.7 ± 2.7 mm and mean width is 24.2 ± 1.3 mm (standard deviation of 2 specimens).

Comparisons. *Rutgersella delawarensis* Johnson & Fox, 1968, from the Early Silurian Shawangunk Formation of eastern Pennsylvania is most similar to these Grindstone Range fossils, but has more deeply impressed ribs and a more elongate central creased depression. *Rutgersella truexi* has a larger central depression and bundled ribs, and *R. kittatinnyensis* a smaller central depression and finer ribbing (Johnson & Fox, 1968). Furthermore, all three Silurian species of *Rutgersella* are preserved as pyritized organic films in dark grey siltstone. The Grindstone Range fossils in contrast, are preserved as external moulds like some Ediacaran–Cambrian discoids and fronds, such as the South Australian, early Cambrian ‘*Swartpuntia*’ sp. of Jensen *et al.* (1998), which they noted is probably a new genus. True *Swartpuntia* from the latest Ediacaran of Namibia (Narbonne *et al.* 1997) and perhaps also the Ediacaran–Cambrian of North Carolina (Weaver *et al.* 2006) is a three-dimensional, large, stiff, and thick-stalked, unlike *Rutgersella* Johnson & Fox, 1968, or ‘*Swartpuntia*’ sp. (of Jensen *et al.* 1998). The lack of definition and regularity, and the wide central depression distinguishes these Grindstone Range fossils from even the most decayed *Dickinsonia*

(Retallack 2007), or other Ediacaran fossils such as *Vendia*, *Praecambridium*, *Yorgia* or *Fractofusus* (Gehling & Narbonne 2007, Fedonkin *et al.* 2007).

Affinities. Cloud (1973) regarded *Rutgersella* as a marcasite ‘sun’ (mineral growth), and thus a pseudofossil. The examples of marcasite suns he illustrated are dissimilar in showing a point centre of mineral growth coplanar with rigid radiating crystals. *Rutgersella* in contrast, has ribs curving into an elliptical central region folded out of the bedding plane. My inspection of the type specimens of *Rutgersella* confirms Cloud’s observations of cubic pyrite (probably diagenetic). There is also biogenic (framboidal) pyrite, and pyrite is scattered within a highly compacted and deformed organic matrix, unlike the brassy, thick, rigid and radiating crystals of true marcasite suns. In contrast, there is no trace of sulfides on the Grindstone Range Sandstone fossils described here.

Rutgersella was considered by Johnson & Fox (1968) a jellyfish of an extinct group that included the Ediacaran fossil *Dickinsonia*. The latter genus has subsequently been regarded as an annelid or other worm, anemone, placozoan, xenophyophore foraminifer, fungus or lichen (Retallack 2007, Sperling *et al.* 2008). *Swartpuntia* has been considered an alga, annelid, sea pen or extinct vendobiont (Narbonne *et al.* 1997), with mushroom or lichen also plausible (Retallack 1994).

Material. P42293, P42332 from Wilpi pedotype in Ten Mile Creek.

Spriggia Sun, 1986

Spriggia wadea Sun, 1986 (Figs 3A; 4A)

Description. *Spriggia wadea* is an annulate, discoid, external mould protruding from the surface of sandstone slabs. Its fine

concentric ridges are more marked than straight and thin radiating ribs. The Grindstone Range fossils have an external diameter of 20.1 mm, a diameter within the outer raised ridge of 15.0 mm, and a central pit 3.6 mm in diameter.

Comparisons. *Spriggia* is not so domed as *Intrites* or *Conomedusites* (Shanker *et al.* 1997), nor does it have multiple ring-like ridges as in *Nimbia* or *Kullingia* (Crimes *et al.* 1995, Crimes & McIlroy 1999, Jensen *et al.* 2002, McIlroy *et al.* 2005). *Spriggia* is flatter than *Aspidella*, with concentric ridges more marked than radial ribs.

Affinities. *Spriggia* has been considered a jellyfish or anemone (Gehling *et al.* 2000), but could also have been a bacterial colony (Steiner & Reitner 2001, Grazhdankin & Gerdes 2007), fungus or lichen (Retallack 1994). Comparable concentric markings have been considered pseudofossil tool marks produced by a tethered object (Jensen *et al.* 2002). However, *Spriggia* has thin radial ribs. It would require an unusual combination of bounce, flexibility and weight to create such fine radial and concentric impressions by rotation.

Material. P42299 from sediment in Ten Mile Creek.

Genera incertae sedis

Branching axes (Figs 5A–B; 6J–K)

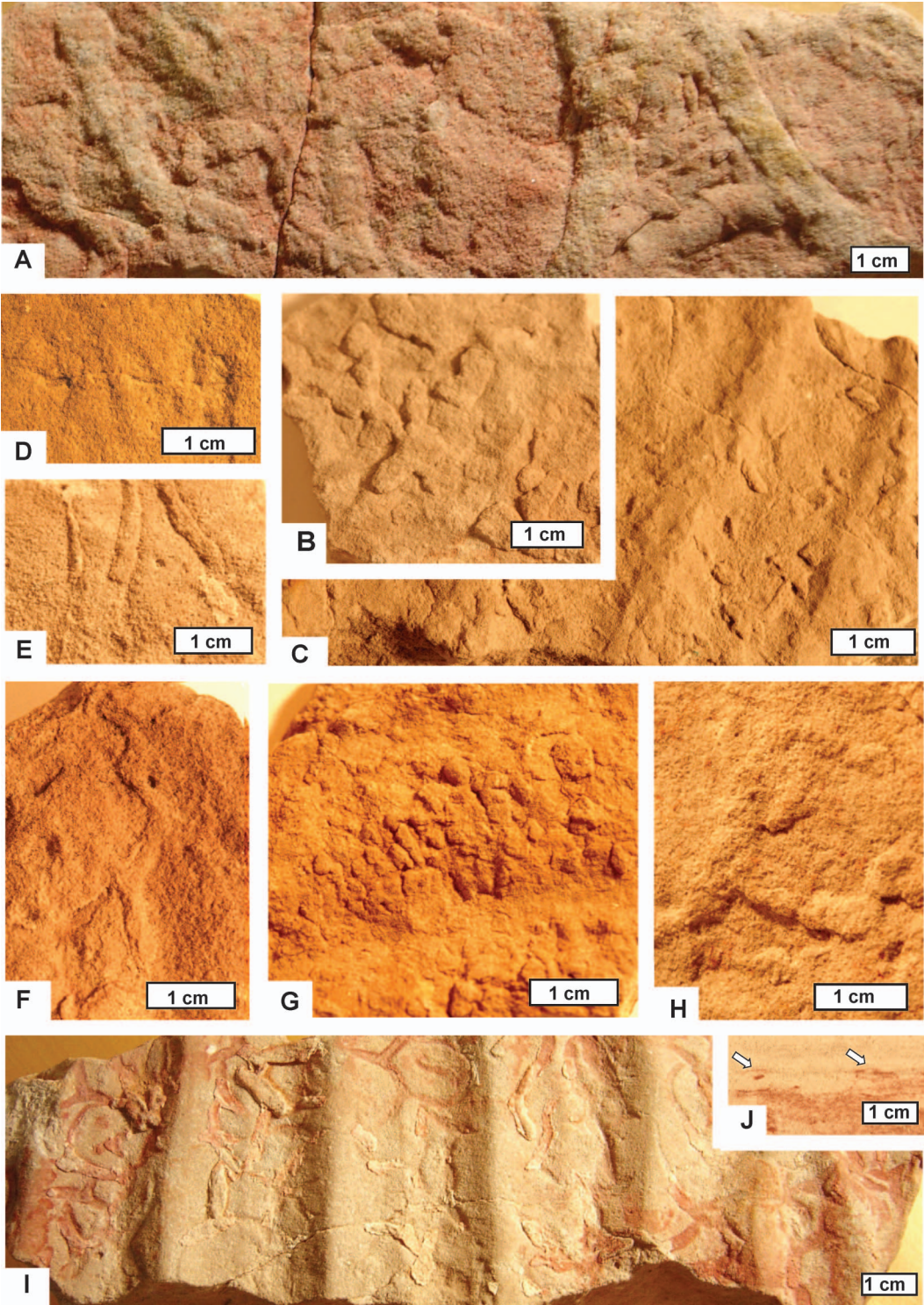
Description. Internal casts of axes up to 20.8 mm in diameter (mean 11.1 ± 8.5 mm for 19) are branched irregularly or dichotomously. Examination in thin-section showed that these are little-compacted, ferruginized casts of large three-dimensional tapering cylinders. Unfortunately, they are not permineralized, but surface impressions examined by SEM are interpreted to reveal a mesh of filaments (Fig. 5A–B).

Comparisons. These large axes are superficially similar to fossil logs and roots of trees, with one (Fig. 6K) showing a dichotomous branch like Pennsylvanian *Stigmaria* and another (Fig. 6J) showing fine branches like roots of Devonian *Callixylon* (Driese & Mora 2001). There is no indication in the Grindstone Range Sandstone fossils of woody fibre, leaf or appendage scars of these well-known fossil tree remains. Poorly preserved, striated, branching casts of large axes like the South Australian specimens have been reported in non-marine rocks of Late Ordovician (Arbey & Koeniguer 1979) and Early Devonian age (Hillier *et al.* 2008), and in both cases were compared with *Prototaxites*. Preservation is not adequate to identify these fossils confidently with permineralized *Prototaxites* from Silurian and Devonian rocks (Hueber 2001, Boyce *et al.* 2007).

Affinities. *Stigmaria* was a lycopsid tree and *Callixylon* a progymnosperm tree (Driese & Mora, 2001), but the Grindstone Range Sandstone fossils lack the anatomy and surface features of these Devonian–Carboniferous plants. *Prototaxites loganii* and *P. southworthii* are now interpreted to be fungi, perhaps basidiomycete (Hueber 2001) or lichenized (Retallack 1994), rather than conifers (Dawson 1859). Fungal affinities are consistent with thin (mean 0.7 ± 0.2 mm for 3) branching extensions of one specimen (Fig. 6J). These may have been rhizine-like, even though these specimens were found not in growth position within palaeosols like comparable fossils described by Arbey & Koeniguer (1979) and Hillier *et al.* (2008), but in bedded sandstone.

Material. P42290, P42291, P42322 from sediment in Ten Mile Creek; P42339 from sediment in Balcoracana Creek.

Ovoid structures (Fig. 6H)



Downloaded By: [Retallack, Gregory J.] At: 18:34 2 November 2009

Description. Ovoid structures averaging 3.1 mm in long axis (± 0.9 mm for 12) are arranged along an axis, and preserved as ferruginized casts with considerable relief.

Comparisons. This specimen looks superficially similar to a fertile early land plant, such as Early Devonian *Zosterophyllum divaricatum* (Gensel 1982). However, the Grindstone Range Sandstone fossil has inflated and compaction-resistant, ovoid bodies, unlike hollow sporangia, and lacks the vascular strand of this early land plant. This fossil appears to be something new, and is illustrated to stimulate recognition of more informative material.

Affinities. *Zosterophyllum* is an early land plant (Zosterophyllophyta), but the compaction resistance of this fossil is more like a fungal fruiting body, especially ascomycete apothecia (Retallack 1994).

Material. P42280 from Upi pedotype in Ten Mile Creek.

Circular structure (Fig. 6I)

Description. A circular structure 9.2 mm in diameter (Fig. 6I) with well-spaced, radiating ribs from an attached axis is preserved as a shallow external mould.

Comparisons. This fossil has the superficial appearance of the Early Devonian land plant *Sciadophyton laxum* (Remy *et al.* 1980), but lacks evidence of a vascular trace. This fossil also may be something new.

Affinities. *Sciadophyton* is a compression fossil comparable with permineralized early

land plant (Rhyniophyta) gametophytes, such as *Kidstoniophyton discoides* and *Langiophyton mackei* (Remy *et al.* 1993), and is an unlikely identification for this fossil, which lacks a vascular trace and plausible associated sporophytes. The well-spaced ribs and outer margin of the fossil penetrate vertically into the sediment, hence showing considerable compaction resistance. The general appearance of this fossil is like a fungal fruiting body, such as a mushroom (Retallack 1994).

Material. P42273, P42274 from Upi pedotype in Ten Mile Creek.

Systematic ichnology

Cochlichnus Hitchcock, 1858

Cochlichnus anguineus Hitchcock, 1858 (Fig. 9F)

Description. *Cochlichnus anguineus* is preserved as sinuous hypichnial ridges after burrows. It lacks texturally differentiated walls and has burrow fill similar to matrix (Aceñolaza & Tortello, 2003).

Comparison. These burrows average 4.0 mm (± 0.4 mm for 11) wide, about four times the width of *Cochlichnus serpens* (Webby 1970). *Cochlichnus antarcticus* and *C. annulatus* are distinguished from the other two species by their lateral markings (Buatois *et al.* 1997).

Trace maker. This trace has been considered the feeding trail of a worm-like creature. Although widely considered a marine trace fossil, *Cochlichnus* also is found in non-marine rocks (Hasiotis 2002).



Fig. 9. Trace fossil burrows of worm-like creatures from the Grindstone Range Sandstone in Ten Mile Creek: **A–B**, *Palaeophycus tubularis* (P42321, P42307 respectively); **C, E**, *Palaeophycus heberti* (P42308, P42345, respectively); **D**, *Planolites montanus* (P42296); **F**, *Cochlichnus anguineus* (P42342); **G–H**, *Torrowangea rosei* (P42343, P42281, respectively); **I–J**, *Myrowichnus arenaceus* (P42258 bedding plane, P42259 cross-sections, respectively).

Material. P42348 from strata in Ten Mile Creek; P42342 from Wilpi pedotype in Ten Mile Creek.

Diplichnites (Dawson) emend. Briggs *et al.* 1979

Diplichnites gouldi (Gevers) Bradshaw, 1981 (Fig. 10A–B, E)

Description. *Diplichnites gouldi* is preserved as concave epichnia of rounded to irregular-equant pits in two more or less parallel rows

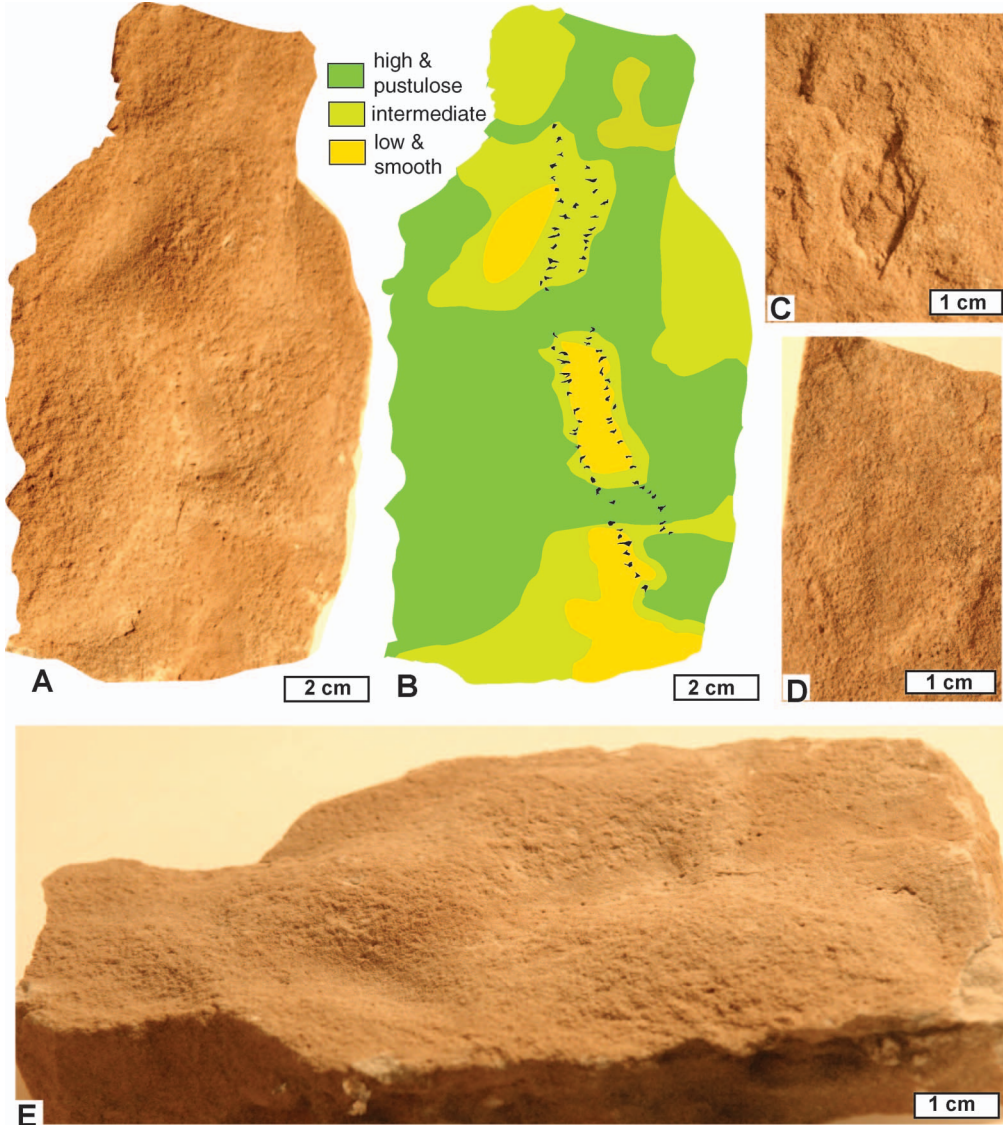


Fig. 10. Arthropod trace fossils from the Grindstone Range Sandstone in Ten Mile Creek, South Australia: A–B, E, *Diplichnites gouldi* (P422286) arthropod trackway in vertical (A) and oblique view (E), and map (B) of biological crust (high) and puddles (low); C–D, *Selenichnites* sp. indet. (P42287, P42354, respectively) arthropod resting traces.

(Trewin & McNamara 1994, Morrissey *et al.* 2004). The outside width of the Grindstone Range trackway averages 15.8 mm (± 0.3 for 4) and its inside width is 9.9 mm (± 0.1 for 4). Mean footprint length is 1.7 mm (± 0.4 for 28). The width of the trail varies slightly with a wavelength of about 8–11 footprints, suggesting that many appendages were borne on each side of the tracemaker.

Comparison. These trackways are small compared with the type material of *D. gouldi* (20–220 mm wide: Bradshaw 1981) and other occurrences of this species (Neef 2004a), but within the size range of some collections of this ichnospecies (Form A of Trewin & McNamara 1994, Wright *et al.*, 1995, Morrissey & Braddy 2004). Larger trackways (200–360 mm wide) of comparable form can be assigned to other ichnospecies, such as *D. cuithensis* Briggs *et al.*, 1979 and *D. aenigma* Dawson, 1873.

The simple near-equant footprints of *Diplichnites gouldi* contrast with elaborately lobate and spiky footprints of other arthropod trackways such as *Kouphichnium*, *Arachnomorphichnus*, *Homopodichnus*, *Caridoidichnus*, *Merostomichnites*, *Orchesteropus*, *Palmichnium*, *Permichnium* and *Tasmanadia* (Häntschel 1975, Fischer 1978, Buatois & Mángano 1993a, Neef 2004b, Weber & Braddy 2004). There is no evidence of median drag marks characteristic of *Oniscoidichnus*, *Palaeohelcura*, *Palmichnium*, *Siskemia* or *Stiaria* (Braddy & Almond 1999, Neef 2004b, Davies *et al.* 2006).

Trace maker. A specimen from Balcoracana Creek (P42352) is a faint trackway in sandstone with a parting lineation fabric formed under water. Another specimen from Ten Mile Creek (P42286) varies considerably in depth and clarity of footprints along its length, and disappears when it crosses surfaces of *Rivularites*, here interpreted as biological soil crust.

Although *Diplichnites* has been considered a trilobite walking trail and thus marine (Häntschel 1975), the emended ichnogenetic diagnosis of Briggs *et al.* (1979) excludes elongated and poorly impressed footprints of trilobites. Arthropleurids (Arthropleurida, Myriapoda), millipedes (Diplopoda, Myriapoda), centipedes (Chilopoda, Myriapoda), eurypterids (Eurypterida, Chelicerata) and euthycarcinoids (Euthycarinoidea, Crustacea) have been proposed as makers of *Diplichnites gouldi* (Trewin & McNamara 1994, Johnson *et al.* 1994, Morrissey & Braddy 2004). Eurypterids are unlikely track-makers considering lack of body-drag marks over very uneven ground and bundles of 8–11 footprints (Fig. 10E). The middle Cambrian myriapod *Cambropodus* (Diplopoda, Scutigermorpha? Robison 1990) is too sprawling and gracile to have made such deep, focused impressions (Fig. 10A, E). The late Cambrian myriapod *Xanthomyria* (Archipolypoda, Diplopoda?; Budd *et al.* 2001) is very elongate, and would make trackways with footprints in strictly parallel curving rows, broadly similar to trackways illustrated by Johnson *et al.* (1994). In contrast, the Grindstone Range specimen has footprints bundled in groups of 8–11 (Fig. 10A, B). This observation together with associated arthropod resting traces of *Selenichnites* sp. indet., are evidence that these trackways were most likely traces of euthycarcinoids.

Material. P42286 from Wilpi pedotype in Ten Mile Creek; P42352 from sediment in Balcoracana Creek.

Myrowichnus gen. nov.

Type species. *Myrowichnus horizontalis* (Myrow, 1995) comb. nov.

Type locality. Fountain Creek and highway 24 at the western end of

Manitou Springs, El Paso County, Colorado, USA: upper Peerless Formation (late Cambrian) and lower Manitou Formation (Early Ordovician).

Diagnosis. Burrows subhorizontal, forming incomplete polygonal networks 2–15 cm below planar exposure or hardground surfaces; walls simple and sharply defined, but with micritic or ferruginous diagenetic cementation extending outward up to another burrow width; Y and T junctions of burrows unexpanded and without subvertical offshoots; burrow fill of red to brown sand, silt or calcite.

Etymology. In honour of Paul Myrow, Colorado College, who described the type species.

Discussion. Myrow (1995) originally attributed *M. horizontalis* to *Thalassinoides* (Ehrenberg) emend. Kennedy, 1967, but noted three clear differences from that genus: (1) thick, diagenetically cemented, rather than simple walls, (2) subhorizontal, rather than three-dimensional arrangement of galleries, and (3) uninflated burrow junctions. Other species of *Thalassinoides* are larger, and have swollen branch-nodes and associated living chambers and vertical or inclined passages not seen in either *M. arenaceus* or *M. horizontalis*. The burrower of *Myrowichnus* reoccupied the burrow in a systematic pattern broadly similar to *Palaeodictyon* (Häntschel 1975), but neither the Grindstone Range nor Colorado fossils show such complete polygonal networks as *Palaeodictyon*.

Myrowichnus horizontalis and *M. arenaceus* are not only similar morphologically, but both are abundant within a narrow (15 cm) horizon immediately below a ferruginized plane, interpreted as a hardground or exposure surface in a carbonate tidal flat in the case of *M. horizontalis* (Myrow 1995), and as a playa palaeosol

surface in the case of *M. arenaceus* (Retallack 2008). Both have a thick cemented zone flanking the burrow, micritized in the case of *M. horizontalis*, and ferruginized in the case of *M. arenaceus*. Both also have more oxidized fill than their matrix: brown dolomite and red calcite spar geopetal structures in the case of *M. horizontalis*, and red siltstone in the case of *M. arenaceus*.

***Myrowichnus arenaceus* sp. nov.** (Fig. 9I–J)

Holotype. P42258 from Upi pedotype in Ten Mile Creek.

Derivation. Latin *arenaceus* meaning sandy.

Diagnosis. *Myrowichnus* burrows in sandstone, 3–5 mm wide, with red clayey alteration halo extending 1 mm into matrix; gently curved subhorizontal burrows dichotomizing at angles of about 60° after intervals of 5–7 burrow widths, but not forming regular polygonal networks; whole burrow system confined to a vertical interval of <15 cm within sediment.

Description. *Myrowichnus arenaceus* is preserved as epichnial grooves and endichnial tubes, commonly curving outward from dichotomies of a network, and usually with a central white sandy fill (mean width 2.6 ± 0.4 mm for 30) within walls ferruginized thickly (extending overall width to 3.6 ± 0.7 mm for 30: see also Fig. 8A–F).

Comparisons. These specimens are most like early Cambrian *Myrowichnus horizontalis* (Myrow 1995) comb. nov., which is larger (9.9 ± 1.9 mm external width). Also similar is *Thalassinoides* sp. indet. in the fluviodeltaic Major Mitchell Sandstone (Silurian) of Victoria, Australia (Gouramanis *et al.* 2003), which lacks the copious branching of the Grindstone Range specimens.

Trace maker. Decapod crustacea are commonly found in generally similar *Thalassinoides* burrows in Devonian and younger marine and intertidal rocks, but both known ichnospecies of *Myrowichnus* predate evolution of decapods (Myrow 1995). Evidence against an arthropod burrower for the Grindstone Range *Myrowichnus* is normal size distribution like that of a soft-bodied creature such as a worm (Fig. 8B), in contrast to the polymodal size distribution of burrows of arthropods growing in instars within Ordovician palaeosols (Retallack 2001).

Material. Upi palaeosols show abundant cross-sections of *Myrowichnus* (Retallack 2008), but only two specimens were exposed extensively in plan view: P42258, P42259, from the Upi pedotype in Ten Mile Creek

Palaeophycus (Hall) emend. Pemberton & Frey, 1982

Palaeophycus heberti (Saporta) Saporta & Marion, 1883 (Fig. 9C, E)

Description. *Palaeophycus heberti* is a smooth and thick-walled burrow with mean width 3.1 mm (standard error ± 1.0 mm for 47 specimens), preserved as endichnial tubes and hypichnial ridges, and with fill similar to that of the matrix (Pemberton & Frey 1982).

Comparisons. Other ichnospecies such as *Palaeophycus alternatus*, *P. annulatus*, *P. canalis*, *P. crenulatus*, *P. striatus*, *P. ferrovittatus*, *P. subornatus* and *P. sulcatus* all differ from *P. heberti* and *P. tubularis* in lacking smooth walls (Fillion & Pickerill 1990, Mángano *et al.* 1996).

Trace maker. The 500 burrows from the type Upi palaeosol measured in the field do not show a polymodal distribution

like that of arthropod burrowers, which grow in instars (Retallack 2001). Instead, they have a normal distribution like that of a soft-bodied burrower, such as a worm (Fig. 8A).

Material. P42278, P42279 from Upi pedotype in Ten Mile Creek; P43389, P42343 from Wilpi pedotype in Ten Mile Creek; P42306, P42308, P42346 from sediment in Ten Mile Creek.

Palaeophycus tubularis Hall, 1847 (Fig. 9A–B)

Description. *Palaeophycus tubularis* is a smooth and thin-walled burrow, preserved as hypichnial ridges, with fill similar to that of the matrix (Pemberton & Frey 1982). The Grindstone Range examples have a mean width of 6.8 mm (± 1.1 mm for 68 specimens).

Comparisons. Some specimens of *P. tubularis* (Fig. 9B) probe and return from short alternating passages in a manner broadly similar to *Treptichnus* (Buatois & Mángano 1993b), but lack the three-dimensional feather-and-stitch pattern of that ichnogenus.

Trace maker. *Palaeophycus tubularis* was probably a feeding trace of a worm-like creature living in water-saturated sediment (Pemberton & Frey 1982). Although widely considered marine, *P. tubularis* is also known from non-marine rocks (Morrissey & Braddy 2004, Ekdale *et al.* 2007). In addition to lake and sea bottom habitats, the occurrence of this ichnospecies deep within Upi palaeosols opens the possibility of life in saturated soil below the water-table (Retallack 2008).

Material. P42282, P42277, P42321, P42344 from Upi pedotype in Ten Mile Creek; P42304, P42305, P42307, P42351 from Wilpi pedotype in Ten Mile Creek.

Planolites Nicholson, 1873

Planolites montanus Richter, 1937 (Fig. 9D)

Description. These burrows are preserved as an endichnial tubes with clay-rich internal texture distinct from their sandy or silty matrix (Pemberton & Frey 1982). Grindstone Range specimens have a mean width of 1.3 mm (± 0.2 mm for 12 specimens).

Comparisons. Other ichnospecies, *Planolites annularis*, *P. constriannulatus* and *P. terraenovae* are banded or striated, and *P. beverleyensis* is larger than *P. montanus* (Fillion & Pickerill 1990; Mángano *et al.* 1996).

Trace maker. *Planolites* is found in both marine and non-marine rocks (Ekdale *et al.* 2007), and was most likely a worm-like, burrowing, deposit-feeder.

Material. P42296, P42309 from Wilpi pedotype in Ten Mile Creek.

Rivularites Fliche, 1906

Rivularites repertus Fliche, 1906 (Fig. 6L–M)

1906 *Rivularites repertus* Fliche, p. 46, pl. III, fig. 4.

1991 ‘old-elephant-skin texture’, Fedonkin in Runnegar & Fedonkin, figs 7.5.2B, 7.5.7F.

1999 ‘elephant skin’ bed-surface texture’, Gehling p. 44, fig. 3A–B.

2000 ‘dimpled sandstone surface’, Gehling p. 76, figs 7d,h.

2000 ‘elephant skin’ texture’, Gehling *et al.* Plate I, figs 1, 5.

2007 ‘elephant skin’ structure’, Fedonkin *et al.* p. 110, fig. 187.

Description. This ichnospecies includes pustulose, undulose, finely ridged, and cracked

surfaces of sandstone slabs, with the general appearance of old elephant skin or poorly laid carpet. Sutured cracks (extending below bed surface) and ridges (protruding from bed) are especially characteristic. These cracks and ridges have the appearance of desiccation cracks swelled shut upon subsequent rehydration, or pressure ridges from lateral intergrowths of radially growing microbial colonies (Fig. 6M). Other features are marked microrelief (Fig. 10E) not always following underlying ripple marks, effective masking of underlying bed forms (Fig. 10E; ‘non-transparent’ *sensu* Noffke *et al.* 2001a, 2006), and craters and peaks of various sizes (Fig. 6M; ‘dimples’ *sensu* Gehling 2000). Finally, horizons of *Rivularites repertus* can be traced laterally for tens of metres in outcrop, and define Wilpi palaeosols (of Retallack 2008), separating beds with ripple marks, lamination, and other purely sedimentary structures.

Comparisons. *Rivularites repertus* Fliche, 1906 and *Kinneyia simulans* Walcott, 1914 are pustulose and wrinkled (respectively) bedding planes, both regarded as pseudofossils by Häntschel (1975). Similar non-biogenic structures include stylolites (Shaub 1939), rain-sculpted surfaces and adhesion warts (Olsen *et al.* 1989). Wilpi palaeosols with laterally continuous *Rivularites* surfaces lacked clay, carbonate, or salts to generate comparable irregularly corroded, or crusted surfaces. Wilpi palaeosols had a highly quartzose composition (Table 1) and must originally have been bound by organic matter, subsequently lost to burial decomposition (Retallack 1997), so that they cracked like clay (Fig. 6L). *Rivularites* also lacks the asymmetry of adhesion warts sculpted by wind or rain, or the relict linear arrangement of moist ripples dissected by wind and rain erosion (Olsen *et al.* 1989). The striated surfaces of stylolites also are absent (Shaub 1939).

Kinneyia is now considered an aquatic algal mat (Hagadorn & Bottjer 1997),

Pedo-type	Diagnosis	Palaeoclimate	Former biota	Palaeo-topography	Parent material	Time for formation
Adla	Red sand (A) over shallow (<50 cm) calcareous nodules (Bk)	Semi-arid (300–500 mm MAP)	Uncertain	Low alluvial terrace and floodplain	Quartz-rich sand	500–1000 yrs
Matarra	Red sand (A) above shallow (<20 cm) crystals of gypsum (By)	Arid (100–300 MAP), evapotranspiration high	Uncertain	Floodplain playa lake	Quartz-rich sand	100–500 yrs
Upi	White sand with red burrows (<i>Myrowichnus</i>) and bedding (A)	Not relevant	Polsterland	Alluvial levee and point bar	Quartz-rich sand	5–10 yrs
Wandara	Ferruginized sandstone (A) over bedded sand	Not relevant	Uncertain	Alluvial levee and point bar	Quartzofeld-spathic sand	5–10 yrs
Wilpi	White sandstone with 'old-elephant skin texture' (<i>Rivularites</i> , A)	Not relevant	Microbial earth	Alluvial levee and point bar	Quartz-rich sand	5–10 yrs

Table 1. Palaeosols of Cambrian–Ordovician Grindstone Range Sandstone. Note: These palaeosols were fully described, classified and interpreted by Retallack (2008).

similar to modern intertidal microbial mats (Noffke *et al.* 2001b). Like *Rivularites*, it also warrants a trace fossil name, in the same way as stromatolites have parataxonomic names (Bertrand-Sarfati & Walter 1981). *Rivularites repertus* specimens of Fliche (1906) have pustules of various sizes, that may include craters, spikes, narrow ridges and irregular edges. *Rivularites permianensis* White, 1929, differs from *R. repertus* in the larger size of its rounded pustules, but also features sharp ridges cast in original matrix. *Rivularites repertus* has been widely noted as 'old elephant skin texture' (Runnegar & Fedonkin 1991).

Affinities. There is no evidence that *Rivularites repertus* included its namesake living cyanobacterium *Rivularia*. *Rivularites* is an ichnogenus for microbial communities of unknown microbial affinities. The sharp sutured cracks and ridges of *R. repertus* are distinct from microbial mat ichnogenera, such as *Kinneyia*, *Eoclathrus* and *Neantia* (Häntschel 1975). Collectively, these three ichnogenera differ from *Rivularites* in their smooth wrinkles or mounds, and may have formed as subaqueous microbial mats that expanded with hydration and lifted from their substrate (Hagadorn & Bottjer 1997, Noffke *et al.* 2001b, Seilacher 2008). In contrast, the sharp and sutured cracks and ridges of *Rivularites repertus* resemble biological soil crusts, in which cracks are sutured by continued growth within a dry matrix, and upward growth is severely curtailed by wind and desiccation (Belknap & Lange 2003). Wide desiccation cracks part some surfaces of *R. repertus* (Fig. 6L). As argued by Prave (2002) for broadly similar Neoproterozoic examples, microbial binding explains how loose sand can crack like clay on drying and exposure. Other deeply cracked, microbially textured sandstones were illustrated by Gehling (2000) and Noffke *et al.* (2006).

Material. This cracked and wrinkled carpet-like trace fossil is very common, but only the following specimens were archived: P42283 from Upi pedotype in Ten Mile Creek; P42260, P42286 from Wilpi pedotype in Ten Mile Creek.

Selenichnites Romano & Whyte, 1990

Selenichnites sp. indet. (Fig. 10C–D)

Description. These are complex depressions on the tops of slabs showing a faint lunate anterior ridge followed by a series of bilaterally symmetrical transverse furrows, akin to resting impressions of arthropods. Furrows are arrayed symmetrically around a shallow axial depression a quarter of the width of the whole impression. Some specimens are shallow (Fig. 10D), whereas others have a deep impression of a narrow axial segmented region (Fig. 10C). They have a mean length of 33.9 ± 7.4 mm, and mean width of 16.9 ± 6.6 mm (5 specimens). A terminal spike-like impression is visible on one specimen (Fig. 10C), but unclear on another (Fig. 10D).

Comparison. These remains are most like *Selenichnites antarcticus* (Weber & Braddy 2004), which differs from other species of *Selenichnites* in having long and thin body impressions behind a weakly marked anterior lunate ridge. *Selenichnites antarcticus* is larger (15–50 mm wide) than the Grindstone Range fossils and lacks a terminal spike-like impression. The type species of the ichnogenus, *S. hundalensis* has a terminal spike-like impression but no more than 10 segments (Romano & Whyte 1987, 1990). *Selenichnites rossendalensis* (Hardy 1970), *S. cordoformis* (Fischer 1978), *S. bradfordensis* (Chisholm 1985), *S. langridgei* (Trewin & McNamara 1994) and *S.* sp. indet. (Draganits *et al.* 2001, Morrissey & Braddy 2004) have only lunate impressions, and no clear body or appendage impressions.

Trace maker. *Selenichnites* has been attributed to resting and feeding by horseshoe crabs (Chelicerata, Xiphosura: Hardy 1970, Chisholm 1985, Romano & Whyte 1987, Draganits *et al.* 2001) and phyllocarids (Crustacea, Phyllocarida: Weber & Braddy 2004), but Trewin & McNamara (1994) also suggested euthycarcinoids (Crustacea, Euthycarinoidea). A euthycarcinoid attribution is most likely for *Selenichnites* sp. indet. described here because of its terminal spike-like impression, numerous segments and axial ridge. Its shape and size are intermediate between the middle Cambrian euthycarcinoid *Apankura* (Vaccari *et al.* 2004) and the Late Ordovician *Kalbarria* (McNamara & Trewin 1993: see Retallack 2009 for revised age).

Material. P42333, P42352, P42354, P42287, P42298 from Wilpi pedotype in Ten Mile Creek.

Torrowangea Webby, 1970

Torrowangea rosei Webby, 1970
(Fig. 9G–H)

Description. These hypichnial ridges are segmented burrow-like tubes with a mean width of 4.5 mm (± 0.9 mm for 20).

Comparison. *Streptichnus* (Jensen & Runnegar 2005) is a similar burrow, but its swellings have a helicoidal ridge unlike these fossils.

Trace maker. *Torrowangea* is commonly associated with *Aspidella*, and could be its burrow if the latter is considered a cnidarian (Gehling *et al.* 2000), or its fruiting body if considered a fungus or lichen (Retallack 1994). Another plausible fungal structure with markedly more constricted beads (Fig. 6H) is preserved as a ferruginized cast, rather than passively filled with sand like *Torrowangea*.

Material. P42280 from Upi in Ten Mile Creek; P42343 from Wilpi in Ten Mile Creek.

Biological and ecological interpretations

Trace and body fossils of the Grindstone Range Sandstone offer unprecedented evidence of Cambrian–Ordovician non-marine biotas (Retallack 2000), distinctly different from Late Ordovician life on land (Retallack 2001). Most of the fossils described here are problematic and poorly preserved. The following interpretations and comparison with modern soil crust communities (Fig. 11) are based in part on their occurrence in palaeosols (Retallack 2008), as outlined below.

Palaeosols and fluvial facies

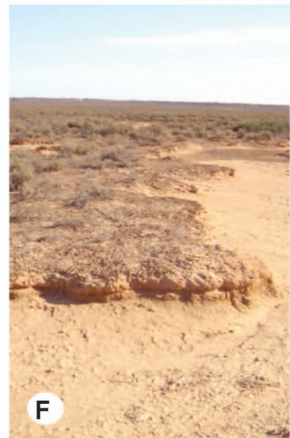
Comparisons of some of the fossils in the Grindstone Range Sandstone with presumed marine fossils has been unavoidable because few non-marine fossils or palaeosols have been recognized in Cambrian rocks (Havlíček 1971, Retallack 2008). Nevertheless, the Grindstone Range Sandstone is not considered a marine deposit for the reasons outlined below.

Like other Ordovician (Caster & Brooks 1956) and Cambrian (Havlíček, 1971) non-marine associations, the assemblage described here includes no definitive marine fossils. Grindstone Range Sandstone fossils are within a sequence of marine regression 1.5 km stratigraphically above the last definitively marine fossil. That fossil is an effaced agnostid trilobite (*?Leipyge laevigata* of Daily & Forbes 1969).

The Grindstone Range Sandstone has thick, basally scoured units of trough cross-bedded sandstone, alternating with flaggy, planar-bedded sandstone with straight-crested ripples. These have been interpreted

as fluvial channels, floodplain and wind ripples, respectively. Interbedded red siltstones include desiccation cracks and

gypsum crystals like those of floodplain and playa deposits (Stock 1974, Moore 1990).



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Many beds within the sandstone have been interpreted as palaeosols (Retallack 2008) based on distinctive soil features (peds, caliche) and gradational alteration down from sharp upper bounding surfaces (soil horizons). Soil peds include blocky units of siltstone and fine-grained sandstone defined by sand-filled cracks (ptygmatically folded clastic dikes) or by slickensided clay skins (ferriargillans in terminology advocated by Retallack 1997). Calcareous nodules in some of the palaeosols have replacive and displacive fabrics of soil caliche, and also are organized into diffuse horizons (Bk horizon) a fixed distance below the sharp contact with overlying rocks (top of A horizon). Gypsum crystals also are organized into discrete horizons below, not at, the surface, as in soils (By horizons), but unlike playa and sabkha evaporites (Retallack 2008). The size of such crystals and nodules is known to be related to the age of modern soils, and is used here as a proxy for soil development (Fig. 2: following Retallack 1997). The depth to Bk and By horizon is known to be related to mean annual precipitation, and ecosystem metabolic measures such as productivity (Retallack 2005). These features of the Grindstone Range palaeosols (Fig. 2) are evidence of an arid to semi-arid palaeoclimate and desert biota, such as biological soil crusts (Table 1). Other less developed palaeosols are recognized on the basis of surface oxidation and bedding plane textures comparable with biological soil crusts (ichnospecies *Rivularites repturus*

Fliche, 1906). Five distinct kinds of palaeosols have been described from the Grindstone Range Sandstone (Retallack 2008), but only two of them (Wilpi and Upi pedotypes of Table 1) have yielded fossils (Table 2).

Biological soil crusts

Rivularites repturus (Fig. 6L–M) strongly resembles biological soil crusts (Belknap & Lange 2003), particularly thick crusts of desert shrublands (Fig. 11E). Gradation from thick non-transparent (meaning substrate-obscuring, following Noffke *et al.* 2001a) crusts, to thinner non-transparent carpet-textured crusts and semi-transparent thin crusts (Fig. 11A, C, E) are also seen in Upi (Fig. 6E–F) compared with Wilpi palaeosols (Fig. 6L–M). Cracking of the sandy surface (compare Figs 6L and 11C) is particularly noteworthy, because crusting micro-organisms bind loose sand and cause it to crack on drying more like clay than silt or sand (Prave 2002). Other evidence for subaerial exposure includes sutured cracks and ridges from impinging growth centres (compare Figs 6M and 11A, C), and uneven microrelief of local mounds (compare Figs 10E and 11E). Individual *Rivularites* surfaces definitive of Wilpi palaeosols can be traced up to 120 m laterally in outcrop and represent laterally extensive biostabilized surfaces, rather than local overgrowth of shifting sediments (Retallack 2008). Biological soil crusts are common in dry regions today (Fig. 11), including Ten Mile

←

Fig. 11. Modern biological soil crusts (A, C, E) comparable with Cambrian–Ordovician examples, and their associated modern vegetation (B, D, F) in New South Wales, Australia: A–B, semi-transparent, cracked, soil crust with light-green foliose lichen (*Xanthoparmelia terrestris*), and fecal pellets on red soil between belah (*Casuarina cristata*) trees at Back Creek State Forest 16 km east of West Wyalong (S33.86613° E147.35642°); C–D, non-transparent, cracked, carpet texture, soil 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 (S34.15419° E143.32983°); E–F, non-transparent, cracked, ‘old elephant skin’, soil crust with dark-purple-grey lichens (*Psora decipiens*) between bluebush (*Maireana sedifolia*, *M. pyramidata*) and saltbush (*Atriplex nummularia*) at Lake Mungo National Park (S33.73008° E143.04432°). Pen for scale (A, E) is 8 mm wide, coin for scale (C) is 28.5 mm diameter.

Flaggy sandstone	Wilpi palaeosol	Upi palaeosol
Fluvial overbank facies	Very weakly developed, thin, sandy, unoxidized soil	Weakly developed, sandy, oxidized soil
<i>Aspidella terranovica</i> (common)	<i>Aspidella terranovica</i> (common)	<i>Ediacaria</i> sp. indet.
<i>Spriggia wadea</i>	<i>Rutgersella</i> sp. indet.	<i>Farghera robusta</i> (common)
axes <i>incertae sedis</i>	cf. <i>Ediacaria</i> sp. indet.	ovoids <i>incertae sedis</i>
<i>Diplichnites gouldi</i>	<i>Rivularites repertus</i> (common)	circular <i>incertae sedis</i>
<i>Cochlichnus anguineus</i>	<i>Diplichnites gouldi</i>	<i>Palaeophycus heberti</i>
<i>Palaeophycus heberti</i>	<i>Selenichnites</i> sp. indet.	<i>Palaeophycus tubularis</i>
	<i>Cochlichnus anguineus</i>	<i>Myrowichnus arenaceus</i> (common)
	<i>Palaeophycus heberti</i>	<i>Torrowangea rosei</i>
	<i>Palaeophycus tubularis</i>	
	<i>Planolites montanus</i>	
	<i>Torrowangea rosei</i>	

Table 2. Fossil assemblages of Cambrian–Ordovician Grindstone Range Sandstone.

Creek, where the climate is too dry for full cover of vascular land plants. Also known as cryptogamic earths and microbial earths, the general term biological soil crust is now used because they include not only cyanobacteria, fungi and lichens, but embryophytes such as mosses, liverworts and angiosperms (Belknap & Lange 2003). *Rivularites* in the Grindstone Range Sandstone probably predates the Middle Ordovician (Llanvirnian) appearance of liverwort spores (Gray 1981), and no clear embryophytic fossils were observed.

Ediacaran holdovers

The Grindstone Range Sandstone includes a range of problematic impressions comparable with a well-known natural assemblage of vendobionts (Seilacher 1992) or Ediacaran fossils (Figs 3–4, Gehling *et al.* 2000): *Aspidella terranovica*, cf. *Ediacaria* sp. indet., *Spriggia wadea*. Other equally enigmatic forms are the body fossil *Rutgersella* sp. indet., and the possible trace fossil *Torrowangea rosei* (Fig. 9G–H). Ediacaran fossils persisted into the early Cambrian (Jensen *et al.* 1998, Crimes & McIlroy 1999), middle Cambrian (Conway Morris 1993, Crimes *et al.* 1995, Vanguetaine & Brueck

2005), late Cambrian (Hagadorn *et al.* 2002), Ordovician (Weber & Braddy 2004), Silurian (Johnson & Fox 1968) and Devonian (Conway Morris & Grazhdankin 2005, 2006). The *Aspidella* complex of forms have been considered marine holdfasts of cnidarians (Gehling *et al.* 2000). Alternatively, *Aspidella* could also have been impressions of microbial colonies (Steiner & Reitner 2001, Grazhdankin & Gerdes 2007) or fruiting bodies of lichens or fungi (Retallack 1994, 2007), and these interpretations are compatible with sedimentary facies of rivers and playas (Retallack 2008) for the Grindstone Range Sandstone. *Rutgersella* from Pennsylvania was non-marine to estuarine, because it was found in the lower part of a fluvial formation with no definitive marine fossils (Johnson & Fox 1968). *Torrowangea* has been assumed to be a marine component of Ediacaran faunas, but some specimens are known from intertidal facies (Cloud 1973, Gehling *et al.* 2000). *Rutgersella* has been considered a jellyfish (Johnson & Fox 1968) and *Torrowangea* a worm-like burrow (Webby 1970), but arguments comparable with those advanced by Retallack (2007) could be advanced for affinities with mushrooms or other fungal fruiting bodies, respectively.

Ediacaran fossils remain puzzling even within rocks of Ediacaran age (Fedonkin *et al.* 2007, Retallack 2007).

Old Red predecessors

Rare fossils in the Grindstone Range Sandstone are superficially like fossil axes (Fig. 6J–K), gametophytes and sporangia (Fig. 6H–I) of fungi and land plants from the Old Red Sandstone and other Silurian–Devonian formations (Remy *et al.* 1980, 1993, Gensel 1982, Driese & Mora 2001). None of the Grindstone Range Sandstone fossils shows woody or vascular tissue equivalent to that of early land plants. Nevertheless, relatively large ferruginized axes (Fig. 6J–K) are superficially similar to the giant Silurian–Devonian fungus *Prototaxites* (Hueber 2001, Boyce *et al.* 2007). Scanning electron microscopy of exterior surfaces of the Grindstone Range axes show features interpreted here to represent a woven filamentous texture (Fig. 5A–B), also comparable with permineralized *Prototaxites*. Identification of the Grindstone Range axes remains uncertain, as with comparably preserved Ordovician (Arbey & Koeniguer 1979) and Devonian sandstone casts (Hillier *et al.* 2008). Similarly enigmatic are remains (Fig. 6H–I) superficially similar to Devonian gametophytes and sporangia (Gensel 1982, Remy *et al.* 1993). These have resistance to burial compaction comparable with other fossil fungi (Retallack 1994, 2007), and could be fungal fruiting bodies such as apothecia or mushrooms. Even if these various fossils were fungi related to Devonian forms, better preserved material will be needed to determine taxonomic affinities.

Dichotomizing thalli

The most eye-catching fossils in palaeosols of the Grindstone Range Formation are radially dichotomous to irregularly

branched external moulds of thalli (Figs 6A–G, 7A–E: form genus *Farghera* gen. nov.). These thalli lack cellular detail: only ferruginized silt and sand grains were seen during inspection with an environmental scanning electron microscope (Fig. 5C). Thus, their biological affinities remain unclear. Nevertheless, these new images of megascopic early life on land are important first steps in scientific understanding, as are currently enigmatic images of the surface of Mars. *Farghera robusta* is very common in Upi palaeosols, which had a different biota than the biological soil crusts of Wilpi palaeosols. In the plant formation terminology of Retallack (1992), thalli of *F. robusta* scattered through Upi palaeosols represent a polsterland (scattered non-vascular plants) as opposed to the microbial earth (biological soil crust with only microscopic organisms) of Wilpi palaeosols.

Farghera robusta measurements betray a pattern of indeterminate growth horizontally (skewness of Fig. 8H), yet determinate growth vertically (unskewed in Fig. 8I), as in ground-hugging plants. The polymodal distribution of widths compiled from observations in natural cross-sections (Fig. 8H), reflects favoured widths of thalli of different order. The high variation in thickness and considerable relief of these fossils in deeply buried sandstone (Fig. 8H) are evidence that they were unusually resistant to compaction by overburden.

Comparable thalloid forms are known from parmeliid lichens (Brodo *et al.* 2001), marchantialean liverworts (Smith 1990), and fucoid or dictyotean algae (Graham & Wilcox 2000). Distinctive of the Grindstone Range Sandstone thalli are wide, tubular to tapering, longitudinally striated, extensions, perpendicular to the thallus margin, but arching and branching downward into the matrix (Fig. 6B). At up to 1 mm wide, the extensions are larger than the rhizoids of marchantialean liverworts (Smith 1990). Their tapering and branching is unlike

floats, trichomes or holdfasts of algae (Graham & Wilcox 2000). The tapering thallus extensions are most like rhizines of fruticose lichens (Brodo *et al.* 2001). The considerable relief of *Farghera* external moulds (Fig. 8G, I) in deeply buried sandstones would be unusual for liverworts or algae, but not for lichens with structural chitin (Retallack 1994, 2007). *Farghera robusta* is very similar to living foliose lichens of dry woodland soils (Belknap & Lange 2003), especially *Xanthoparmelia reptans* (Fig. 11C).

Arthropod traces

One arthropod trackway among the Grindstone Range fossils is thought to have been made on land (Fig. 10A–B, E). Arthropod trackways known to have formed subaqueously (because they are overprinted by fish trails: Morrissey *et al.* 2004, Seilacher 2007) show four features: (1) strong asymmetry (one side current-buoyed more than the other), (2) simple, shallow markings (neither deep, bulging outward nor partially filled with miniature talus cones), (3) little variation in clarity along the length of the trackway (indicating matrix of even hydration and texture) and (4) parallel rather than alternate gait (sculling rather than walking motion). None of these subaqueous features is found in the trackway (*Diplichnites gouldi*) from the Grindstone Range Sandstone.

These various features also are lacking in trackways created under water on substrates of unusually dehydrated or algal-bound clay (personal observations of modern intertidal tracks), but in the Grindstone Range deep impressions were seen only in palaeotopographic lows of smooth sand, interpreted as moist sediment of small, drying puddles. The tracks disappear entirely in raised-pustulose areas and are faint in low-pustulose areas (*Rivularites repertus*), interpreted here as biological soil crust that

cushioned footfalls on palaeosols of the Wilpi pedotype (Retallack 2008).

This evidence of arthropod excursions on land may be the oldest known, although dating is uncertain for these and other plausible subaerial trackways: late Cambrian or Early Ordovician (MacNaughton *et al.* 2002), early Late Ordovician (Caradocian: Johnson *et al.* 1994) and Late Ordovician (Ashgillian: Trewin & McNamara 1994; for revised dating see Retallack 2009). Comparable traces of arthropods on land are widespread in non-marine rocks of Silurian (Wright *et al.* 1995), Devonian (Bradshaw 1981, Morrissey & Braddy 2004) and Carboniferous age (Briggs *et al.* 1979).

Also found in slabs of Wilpi pedotype were arthropod resting impressions (Fig. 10C–D: *Selenichnites* sp. indet.) of a creature about the size of the trackways. The trackways have cycles of 8–11 pairs of limbs, and about 11 appendage furrows are seen in resting impressions. These observations are compatible with a euthycarcinoid tracemaker, such as *Kalbarria* or *Apankura*. The Grindstone Range resting impressions indicate a different creature (Fig. 11), intermediate between middle Cambrian *Apankura* (Vaccari *et al.* 2004), which had limbs extending well beyond the carapace, and Late Ordovician *Kalbarria* (McNamara & Trewin 1993), which was larger, with stronger differentiation of a wide thorax and narrow abdomen.

Euthycarcinoids have limbs with many ring-like segments and few obvious nodules or other irregularities for attachment of large internal muscles. In addition, the limbs are oriented laterally from an axial ridge (Fig. 11). This would not have been as effective for terrestrial locomotion as longer segments of the limbs of myriapods and insects (Manton 1977). Nevertheless, Cambrian euthycarcinoids such as *Apankura* have stout limbs protruding well beyond the carapace (Vaccari *et al.* 2004), and

would be more capable on land than the shorter limbs of Devonian and younger euthycarcinoids (Gall & Grauvogel 1964, Schram & Rolfe 1982). Triassic *Euthycarcinus* had small mandibles and much clay in the gut, suggestive of a sediment-feeding detritivore (Gall & Grauvogel 1964), but middle Cambrian *Apankura* had large sclerotized mandibles and a buccal complex (Vaccari *et al.* 2004) like of those of Crustacea feeding on small live prey (Manton 1977). This is another indication that Cambrian–Ordovician euthycarcinoids may have been more capable on land than geologically younger euthycarcinoids.

Putative terrestrial euthycarcinoid trails described here and elsewhere (Trewin & McNamara 1994) are more likely the result of short excursions of amphibious creatures, rather than of fully terrestrial animals. Amphibious behaviour accounts for the lack of any likely arthropod burrows in palaeosols of the Grindstone Range Formation. Ephemeral streams and playa lakes are compatible with sedimentological interpretations of the Grindstone Range Sandstone (Stock 1974, Moore 1990), and Upi palaeosols have oxidized burrows within chemically reduced matrix similar to soils with perennially high water-table near lakes (Retallack 2008).

Other animals

Other trace fossils also were found in the Grindstone Range Sandstone: *Cochlichnus anguineus*, *Palaeophycus heberti*, *Palaeophycus tubularis*, *Planolites montanus* and *Myrowichnus arenaceus*. Measurements of 500 *Myrowichnus arenaceus* burrows show a normal size distribution, unlike the polymodal distribution of arthropod burrows (Retallack 2001), so were most likely the work of soft-bodied, worm-like creatures. Their palaeosols and host sediments are superficially ferruginized, but largely unoxidized, so were wet soils and sediments that

were often waterlogged (Retallack 2008). *Cochlichnus*, *Palaeophycus* and *Planolites* are known in both marine and lacustrine sediments (Hasiotis 2002, Ekdale *et al.* 2007). *Myrowichnus* is known elsewhere from beneath intertidal ferruginized hardgrounds or exposure surfaces (Myrow 1995).

As an assemblage (Table 2), the Grindstone Range Sandstone trace fossils are most like the lacustrine *Mermia* ichnofacies (MacEachern *et al.* 2007), though with different taxa than Carboniferous (Buatois *et al.* 1998) or early Cambrian examples (Mikuláš 1995). Early Ordovician estuarine facies had ichnofaunas dominated by *Merostomichnites* (Weber & Braddy 2004), and shoreface sandstones included *Skolithos* piperock (Mángano *et al.* 1996). Early Ordovician marine ichnofaunas include as many as 30 ichnospecies of traces attributed to trilobites, such as *Cruziana* and *Rusophycus* (Baldwin 1977, Pickerill *et al.* 1984, Fillion & Pickerill 1990, Mángano *et al.* 1996, Aceñolaza & Aceñolaza 2002, Poiré *et al.* 2003). Early Ordovician deep shelf ichnofaunas included *Chondrites* and *Zoophycos* (Mikuláš 1994) and deep marine communities included *Neonereites* and *Helminthopsis* (Crimes *et al.* 1992). Thus, a wide array of marine ichnofacies had evolved by Early Ordovician time, but not all non-marine ichnofacies, because the *Scoyenia* ichnofacies did not appear until the Late Ordovician (Retallack 2001).

Soil communities

Wilpi and Upi palaeosols, which contain most of the trace and body fossils described here, are very weakly developed, thin profiles, with some bedding undisturbed by bioturbation (Fig. 11). Other palaeosols in the Grindstone Range Formation have large calcareous nodules (Adla pedotype) and gypsum crystals (Matarra pedotype) evidencing extended periods (10^4 – 10^5 years)

of soil formation, landscape stability, and arid to semi-arid palaeoclimate (Table 1). These moderately developed palaeosols show less clear indications of life, but this is not surprising for palaeosols. Discrete trace fossils and plant fossils are more common in weakly developed palaeosols than moderately developed palaeosols, which have dominantly pedogenic fabric (Retallack 1998). Moderately developed palaeosols and more humid regions known elsewhere in the Ordovician (Retallack 2000) may have supported larger biomass communities with similar kinds of organisms to those demonstrated here from the early successional palaeosols and associated sediments.

Nevertheless, the lack of burrows in well-drained palaeosols (Adla and Matarra pedotypes of Fig. 11) is significant, especially compared with the abundance of arthropod burrows in Late Ordovician calcareous red palaeosols (Retallack 2001). Also significant is the absence of arthropod burrows in intermittently waterlogged palaeosols (Upi and Wilpi pedotypes): burrows in these palaeosols show a smooth size distribution of worms and other continuously growing animals (Fig. 8). For these reasons, the arthropod track-maker (*Diplichnites gouldi*) was probably amphibious, rather than a permanent land dweller. Fossil eutycarcinoids like those thought to have made these South Australian tracks have been found in marine shales (Vaccari *et al.* 2004) and non-marine sandstones (McNamara & Trewin 1993) and shales (Schram & Rolfe, 1982).

Conclusions

Cambrian–Ordovician landscapes were not entirely barren, because there were visible life forms including amphibious arthropods and sessile thalli (Fig. 12). Palaeosol evidence indicates that these polsterlands (vegetation of scattered non-vascular plants) were

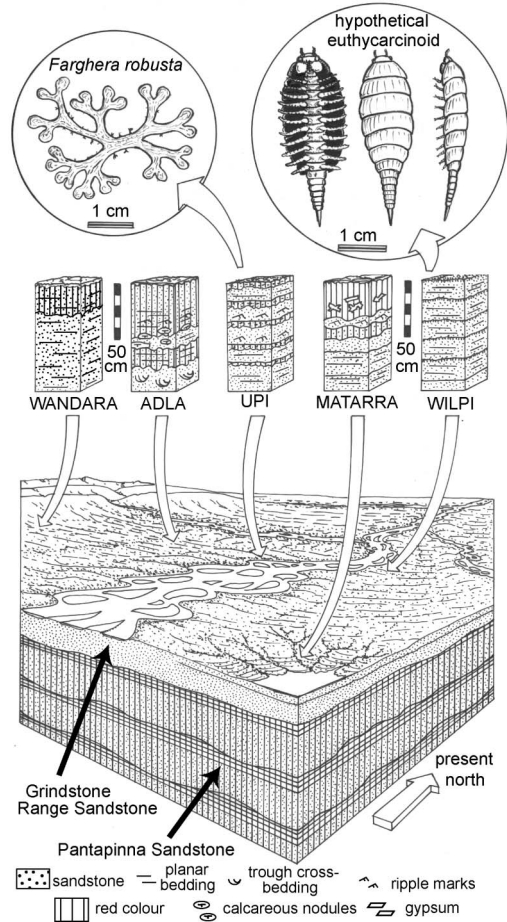


Fig. 12. Reconstructed Early Ordovician (Tremadocian, 583 Ma) landscape, soils, and biota of the Grindstone Range Formation in South Australia.

distinctly different terrestrial communities than liverwort-millipede polsterlands of the Late Ordovician (Retallack 2000, 2001), or trigonotarbid-tracheophyte brake-lands (non-grassy meadow-like vegetation) of the Early Silurian (Retallack 1992, 2001).

Other evidence that Cambrian–Ordovician landscapes were not barren comes from the degree of weathering of Cambrian–Ordovician sandstones (Dott 2003) and clay minerals (Kennedy *et al.* 2006), spores resembling those of land plants (Strother 2000), and sedimentary

facies of subaerial exposure (Rose 2006). Some organic cover was needed to stabilize the landscape for the many millenia needed to produce pedogenic carbonate nodules (Retallack 2005) of the size seen in palaeosols of the Grindstone Range Sandstone and older formations (Figs 2, 12).

Evidence for arthropod excursions on land presented here (Fig. 10) supports the view of Buatois *et al.* (1998) that early arthropods ventured on land to exploit new resources. This is not to deny alternative views of continental excursions into saline groundwater (Maples & Archer 1989), to avoid predation (Trewin & McNamara 1994) and to mate without being disturbed (Braddy 2004). Evidence of deep burrowing in early Cambrian coastal palaeosols (Retallack 2008) supports the idea that some animals lived below the water-table of coastal soils normally dry at the surface (Maples & Archer 1989). Very large Ordovician trackways associated with smaller ones could very well be predator and prey (Trewin & McNamara 1994: see Retallack 2009 for revised dating). The abundance of complex trackways in some nearshore Ordovician–Cambrian sandstones is consistent with mass-mating, as is well known among horseshoe crabs (MacNaughton *et al.* 2002). All of these activities were promoted by increasingly bulky land vegetation, which intensified weathering and nutrient supply to the ocean, as reflected in marine faunal diversification and size increases (Bambach 1993).

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References

- ACEÑOLAZA, G.F. & ACEÑOLAZA, F.G., 2002. Icnología de la Formación Sepulturas (Ordovícico) en el Espinazo del Diablo, Cordillera Oriental de Jujuy, Argentina. *Ameghiniana* 39, 471–499.
- ACEÑOLAZA, G.F. & TORTELLO, M.F., 2003. El Alisal: a new locality with trace fossils of the Puncoviscana Formation (Late Precambrian–early Cambrian) in Salta Province, Argentina. *Geologica Acta* 1, 95–102.
- AGARDH, C.A., 1821. Dictyonema. In *Synopsis plantarum quas in itinere orbis novi collegerunt Al. de Humboldt et Am. Bonpland*, C.S. KUNTH, ed., N. Maze, Paris, 203.
- ARBÉY, F. & KOENIGUER, J.-C., 1979. Les nématophytes et les algues de l'Ordovicien et du Dévonien Saharien. *Centres de Recherches Exploration Production Elf-Aquitaine Bulletin* 3(2), 409–418.
- BALDWIN, C.T., 1977. The stratigraphy and facies association of some Cambrian and Ordovician rocks of northwestern Spain. *Geological Journal Special Issue* 9, 9–40.
- BAMBACH, R.K., 1993. Seafood through time; changes in biomass, energetics, and productivity in the marine ecosystem. *Paleobiology* 19, 372–397.
- BELKNAP, J. & LANGE, O.L. (eds), 2003. *Biological Soil Crusts: Structure, Function and Management*. Springer, Berlin, 503 pp.
- BERTRAND-SARFATI, J. & WALTER, M.R., 1981. Stromatolite biostratigraphy. *Precambrian Research* 15, 353–371.
- BILLINGS, E., 1872. Fossils in Huronian rocks. *Canadian Naturalist and Quarterly Journal of Science* 6, 478.
- BOYCE, C.K., HOTTON, C.L., FOGEL, M.L., CODY, G.D., HAZEN, R.M., KNOLL, A.H. & HUEBER, F.M., 2007. Devonian landscape heterogeneity recorded by a giant fungus. *Geology* 35, 399–402.
- BRADDY, S.J., 2004. Ichnological evidence for the arthropod invasion of land. *Fossils and Strata* 51, 136–140.
- BRADDY, S.J. & ALMOND, J., 1999. Eurypterid trackways from the Table Mountain Group (Lower Ordovician) of South Africa. *Journal of African Earth Sciences* 29, 165–177.
- BRADSHAW, M.A., 1981. Palaeoenvironmental interpretation and systematics of Devonian trace fossils from the Taylor Group (lower Beacon Super-group), Antarctica. *New Zealand Journal of Geology and Geophysics* 24, 615–652.

- BRASIER, M.D. & ANTCLIFFE, J.B., 2008. *Dickinsonia* from Ediacara: a new look at morphology and body construction. *Palaeogeography Palaeoclimatology Palaeoecology* 270, 311–323.
- BRIGGS, D.E.G., ROLFE, W.D.I. & BRANNAN, J., 1979. A giant myriapod trail from the Namurian of Arran, Scotland. *Palaeontology* 22, 273–291.
- BRODO, I.M., SHARNOFF, S.D. & SHARNOFF, S., 2001. *Lichens of North America*. Yale University Press, New Haven, CT, 795 pp.
- BUATOIS, L.A. & MANGANO, M.G., 1993a. Trace fossil from a Carboniferous turbiditic lake: implications for the recognition of additional non-marine ichnofacies. *Ichnos* 2, 237–258.
- BUATOIS, L.A. & MANGANO, M.G., 1993b. The ichnotaxonomic status of *Plangtichnus* and *Treptichnus*. *Ichnos* 2, 217–224.
- BUATOIS, L.A., JALFIN, G. & ACEÑOLAZA, F.G., 1997. Permian non-marine invertebrate trace fossils from southern Patagonia, Argentina: ichnologic signatures and substrate consolidation and colonization sequences. *Journal of Paleontology* 21, 466–472.
- BUATOIS, L.A., MANGANO, M.G., GENISE, J.F. & TAYLOR, T.N., 1998. The ichnologic record of continental invertebrate invasion: evolutionary trends in environmental expansion, ecospace utilization, and behavioral complexity. *Palaios* 13, 217–240.
- BUDD, G.E., HÖGSTRÖM, A.E.S. & GOGIN, I., 2001. A myriapod arthropod from the Upper Cambrian of East Siberia. *Paläontologische Zeitschrift* 75, 37–41.
- BUTTERFIELD, N.J., 2005. Probable Proterozoic fungi. *Paleobiology* 31, 165–181.
- CASTER, K.E. & BROOKS, H.K., 1956. New fossils from the Canadian–Chazyan (Ordovician) hiatus in Tennessee. *Bulletins of American Paleontology* 36, 157–199.
- CHALONER, W.G., MENSAH, M.K. & CRANE, M.D., 1974. Non-vascular land plants from the Devonian of Ghana. *Palaeontology* 17, 925–947.
- CHAVES, J.L., LÜCKING, R., SIPMAN, H.J.M., UMAÑA, L. & NAVARRO, E., 2004. A first assessment of the tocolichen biodiversity inventory in Costa Rica: the genus *Dictyonema* (Polyporales: Atheliaceae). *Bryologist* 107, 242–249.
- CHISHOLM, J.I., 1985. Xiphosurid burrows from the Lower Coal Measures (Westphalian A) of West Yorkshire. *Palaeontology* 28, 619–628.
- CLOUD, P.E., 1973. Pseudofossils: a plea for caution. *Geology* 1, 123–127.
- CONWAY MORRIS, S., 1993. Ediacaran-like fossils in Cambrian Burgess shale-type faunas of North America. *Palaeontology* 36, 593–635.
- CONWAY MORRIS, S. & GRAZHDANKIN, D., 2005. Enigmatic worm-like organisms from the Upper Devonian of New York; an apparent example of Ediacaran-like preservation. *Palaeontology* 48, 395–410.
- CONWAY MORRIS, S. & GRAZHDANKIN, D., 2006. A postscript to the enigmatic *Protonympha* (Devonian; New York); is it an arm of the echinoderms? *Palaeontology* 49, 1335–1338.
- CRIMES, T.P. & McILROY, D., 1999. A biota of Ediacaran aspect from Lower Cambrian strata on the Digermul Peninsula, Arctic Norway. *Geological Magazine* 136, 633–642.
- CRIMES, T.P. & HIDALGO, J.F.G. & POIRÉ, D.G., 1992. Trace fossils from Arenig flysch sediments of Eire and their bearing on early colonization of the deep seas. *Ichnos* 2, 61–77.
- CRIMES, T.P. & INSOLE, A. & WILLIAMS, B.P.J., 1995. A rigid-bodied Ediacaran biota from Upper Cambrian strata in Co. Wexford, Eire. *Geological Journal* 30, 89–109.
- DAILY, B. & FORBES, B.G., 1969. Notes on the Proterozoic and Cambrian, southern and central Flinders Ranges. In *Geological Excursions Handbook*, B. DAILY, ed., Australian and New Zealand Association for the Advancement of Science, Section 3, 23–30.
- DALRYMPLE, G.B., 1979. Critical tables for conversion of K–Ar ages from old to new constants. *Geology* 7, 558–560.
- DAVIES, N.S., SANSOM, I.J. & TURNER, P., 2006. Trace fossils and paleoenvironments of a Late Silurian marginal marine/alluvial system: the Ringerike Group (Lower Old Red Sandstone), Oslo region, Norway. *Palaios* 21, 46–62.
- DAWSON, J.W., 1859. On the fossil plants from the Devonian rocks of Canada. *Geological Society of London Quarterly Journal* 15, 477–488.
- DAWSON, J.W., 1873. Impressions and footprints of aquatic animals and imitative markings on Carboniferous rocks. *American Journal of Science* 5, 16–24.
- DEBRENNE, F. & NAUD, G., 1981. Meduses et trace fossiles supposées précambriennes dans le formation San Vito, Sarrabus, Sud-West de la Sardigne. *Bulletin de la Société Géologique de France* 7, 23–31.
- DOTT, R.H., 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.
- DRAGANITS, E., BRADY, S.J. & BRIGGS, D.E.G., 2001. A Gondwanan coastal arthropod ichnofauna from the Muth Formation (Lower Devonian, northern India): paleoenvironment and trace-maker behavior. *Palaios* 16, 126–147.
- DRIESE, S.G. & MORA, C.I., 2001. Diversification of Siluro-Devonian plant traces in paleosols and influence on estimates of paleoatmospheric CO₂ levels. In *Plants Invade the Land: Evolutionary and Environmental Perspectives*, P.G. GENSEL & D. EDWARDS, eds, Columbia University Press, New York, 237–253.

- EKDALE, A.A., BROMLEY, R.G. & LOOPE, D.B., 2007. Ichnofacies of an ancient erg: a climatically-influenced trace fossil association in the Jurassic Navajo Sandstone, southern Utah, USA. In *Trace Fossils: Concepts, Problems, Prospects*, W. MILLER, ed., Elsevier, Amsterdam, 562–574.
- ELBURG, M.A., BONS, P. D., FODEN, J. & BRUGGER, J., 2003. A newly defined Late Ordovician magmatic-thermal event in the Mt. Painter Province, northern Flinders Ranges, South Australia. *Australian Journal of Earth Sciences* 50, 611–631.
- FEDONKIN, M.A., GEHLING, J.G., GREY, K., NARBONNE, G.M. & VICKERS-RICH, P. (eds), 2007. *The Rise of Animals: Evolution and Diversification of the Kingdom Animalia*. Johns Hopkins University Press, Baltimore, MD, 244 pp.
- FILLION, D. & PICKERILL, R.K., 1990. Ichnology of the Upper Cambrian? To Lower Ordovician Bell Island and Wabana Groups of Eastern Newfoundland, Canada. *Palaeontographica Canadiana* 7, 1–119.
- FISCHER, W.A., 1978. The habitat of the early vertebrates: trace fossil and body fossil evidence from the Harding Formation (Middle Ordovician), Colorado. *Mountain Geologist* 15, 1–26.
- FLETCHER, B.J., BEERLING, D.J. & CHALONER, W.G., 2004. Stable carbon isotopes and the metabolism of the terrestrial Devonian organism *Spongiophyton*. *Geobiology* 2, 107–119.
- FLICHE, P., 1906. Flore fossile du trias en Lorraine et en Franche-Comté. *Société des Sciences Nancy Séances* 6, 1–66.
- GALL, J.-C. & GRAUVOGEL, L., 1964. Un arthropode peu connu, le genre *Euthycarcinus* Handlirsch. *Annales de Paléontologie Invertébrés* 50, 1–18.
- GEHLING, J.G., 1999. Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. *Palaios* 14, 40–57.
- GEHLING, J.G., 2000. Environmental interpretation and a sequence stratigraphic framework for the terminal Proterozoic Ediacara Member within the Rawnsley Quartzite in South Australia. *Precambrian Research* 100, 65–95.
- GEHLING, J.G. & NARBONNE, G.M., 2007. Spindle-shaped Ediacaran fossils from the Mistaken Point assemblage, Avalon Zone, Newfoundland. *Canadian Journal of Earth Sciences* 44, 367–387.
- GEHLING, J.G., NARBONNE, G.M. & ANDERSON, M.M., 2000. The first named Ediacaran body fossil; *Aspidella terranovica*. *Palaeontology* 43, 427–456.
- GENSEL, P.G., 1982. A new species of *Zosterophyllum* from the Early Devonian of New Brunswick. *American Journal of Botany* 69, 651–699.
- GENSEL, P.G., CHALONER, W.G. & FORBES, W.H., 1991. *Spongiophyton* from the late Lower Devonian of New Brunswick and Quebec, Canada. *Palaeontology* 34, 149–168.
- GEYER, G. & SHERGOLD, J., 2000. The quest for internationally recognized divisions of Cambrian time. *Episodes* 23, 188–195.
- GOURAMANIS, C., WEBB, J.A. & WARREN, A.A., 2003. Fluviodeltaic sedimentology and ichnology of part of the Silurian Grampians Group, western Victoria. *Australian Journal of Earth Sciences* 50, 811–825.
- GRADSTEIN, F.M., OGG, J.G. & SMITH, A.G., 2004. *A Geologic Time Scale 2004*. Cambridge University Press, Cambridge, 589 pp.
- GRAHAM, L.E. & WILCOX, L.W., 2000. *Algae*. Prentice-Hall, Upper Saddle River, NJ, 430 pp.
- GRAY, J., 1981. The microfossil record of early land plants: advances in understanding of early terrestrialization, 1970–1984. *Royal Society of London Philosophical Transactions B* 309, 167–185.
- GRAVESTOCK, D.I. & SHERGOLD, J.H., 2001. Australian Early and Middle Cambrian sequence biostratigraphy with implications for species diversity and correlation. In *The Ecology of the Cambrian Radiation*, A.Y. ZHURAVLEV & R. RIDING, eds, Columbia University Press, New York, 107–136.
- GRAZHDANKIN, D. & GERDES, G., 2007. Ediacaran microbial colonies. *Lethaia* 40, 201–210.
- HAGADORN, J.W. & BOTTJER, D.J., 1997. Wrinkle structures: microbially mediated sedimentary structures common in subtidal siliciclastic settings at the Proterozoic–Phanerozoic transition. *Geology* 25, 1047–1050.
- HAGADORN, J.W., DOTT, R.H. & DAMROW, D., 2002. Stranded on a Late Cambrian shoreline; medusae from central Wisconsin. *Geology* 30, 147–150.
- HAHN, G. & PFLUG, H.D., 1980. Ein neuer Medusen-Fund aus der Jung-Präkambrium von Zentral-Iran. *Senckenbergiana Lethaea* 60, 449–461.
- HAINES, P.W. & FLÖTTMANN, T., 1998. Delamerian orogeny and potential foreland sedimentation: a review of age and stratigraphic constraints. *Australian Journal of Earth Sciences* 45, 559–570.
- HALL, J., 1847. *Paleontology of New York, v. 1. Containing Descriptions of the Lower Division of the New-York System*. C. van Benthuysen, Albany, NY, 338 pp.
- HALL, J., 1851. Descriptions of new or rare species of fossils from the Paleozoic Series. In *Report on the Geology of the Superior Land District. Part 2. The Iron Region Together with the General Geology*, J.W. FOSTER & I.D. WHITNEY, eds, Government Printer, Washington, DC, 203–231.
- HALLBAUER, D.K. & VAN WARMELO, K.T., 1974. Fossilized plants in tuculite from Precambrian rocks of the Witwatersrand, South Africa. *Precambrian Research* 1, 193–212.
- HALLBAUER, D.K., JAHNS, H.M. & BELTMANN, H.A., 1977. Morphological and anatomical observations on some Precambrian plants from the Witwatersrand, South Africa. *Geologische Rundschau* 66, 477–491.

- HÄNTSCHEL, W., 1975. *Treatise on Invertebrate Paleontology. Part. W. Miscellanea. Supplement 1. Trace Fossils and Problematica*. Geological Society of America & University of Kansas Press, Boulder, CO and Lawrence, KS, 269 pp.
- HARDY, P.G., 1970. New xiphosurid trails from the Upper Carboniferous of northern England. *Palaeontology* 13, 188–190.
- HASIOTIS, S.T., 2002. Continental trace fossils. *Society of Economic Paleontologists and Mineralogists Short Course Notes* 51, 130 pp.
- HAVLÍČEK, V., 1971. Stratigraphy of the Cambrian of central Bohemia. *Sborník Geologických Věd Geologie* 20, 7–52.
- HILLIER, R.D., EDWARDS, D. & MORRISSEY, L.B., 2008. Sedimentological evidence for rooting structures in the Early Devonian Anglo-Welsh Basin (UK), with speculation on their producers. *Palaeogeography Palaeoclimatology Palaeoecology* 270, 366–380.
- HITCHCOCK, E., 1858. *Ichnology of New England: a Report on the Sandstone of the Connecticut Valley, Especially its Footprints*. W. White, Boston, 220 pp.
- HUEBER, F.M., 2001. Rotted wood–alga–fungus; the history and life of *Prototaxites* Dawson 1859. *Review of Palaeobotany and Palynology* 116, 123–158.
- JAGO, J.B., ZANG, W.L., SUN, X.L., BROCK, G.A., PATERSON, J.R. & SKOVSTED, C.B., 2006. Correlation within early Palaeozoic basins of eastern South Australia. *Palaeoworld* 15, 406–423.
- JAHREN, A.H., PORTER, S. & KUGLITSCH, J.J., 2003. Lichen metabolite identified in Early Devonian terrestrial organisms. *Geology* 31, 99–102.
- JENSEN, S. & RUNNEGAR, B.N., 2005. A complex trace fossil from the Spitskopf Member (terminal Ediacaran–?Lower Cambrian) of southern Namibia. *Geological Magazine* 142, 561–569.
- JENSEN, S., GEHLING, J.G. & DROSER, M.L., 1998. Ediacara-type fossils in Cambrian sediments. *Nature* 393, 567–569.
- JENSEN, S., GEHLING, J.G., DROSER, M.L. & GRANT, S.W.F., 2002. A scratch circle origin for the medusoid fossil *Kullingia*. *Lethaia* 35, 291–299.
- JOHNSON, E.W., BRIGGS, D.E.G., SUTHREN, R.J., WRIGHT, J.L. & TUNNIKOFF, S.P., 1994. Non-marine arthropod traces from the subaerial Ordovician Borrowdale Volcanic Group, English Lake District. *Geological Magazine* 131, 395–406.
- JOHNSON, H. & FOX, S.K., 1968. Dipleurozoa from the Lower Silurian of North America. *Science* 162, 119–120.
- JURINA, A.L. & KRASSILOV, V.A., 2002. Lichenlike fossils from the Givetian of central Kazakhstan. *Paleontological Journal* 36, 541–547.
- KENNEDY, M., DROSER, M., MAYER, L.M., PEVEAR, D. & MROFKA, D., 2006. Late Precambrian oxygenation: inception of the clay mineral factory. *Science* 311, 1446–1449.
- KENNEDY, W.J., 1967. Burrows and surface traces from the Lower Chalk of southern England. *British Museum Natural History Geology Bulletin* 15, 125–167.
- KIRSCHVINK, J.L. & RAUB, T.D., 2003. A methane fuse for the Cambrian explosion: carbon cycles and true polar wander. *Geoscience* 335, 65–78.
- LAURIE, J.R., 2006. Ordovician trilobites from the Horn Valley Siltstone and basal Stairway Sandstone, Amadeus Basin, Northern Territory. *Association of Australasian Palaeontologists Memoir* 32, 287–345.
- MACEachern, J.A., PEMBERTON, S.G., GINGRAS, M.K. & BANN, K.L., 2007. The ichnofacies paradigm: a fifty-year retrospective. In *Trace Fossils: Concepts, Problems, Prospects*, W. MILLER, ed., Elsevier, Amsterdam, 52–77.
- MACNAUGHTON, R.B., COLE, J.M., DALRYMPLE, R.W., BRADY, S.J., BRIGGS, D.E.G. & LUKIE, T.D., 2002. First steps on land: Arthropod trackways in Cambrian–Ordovician eolian sandstone, southeastern Ontario, Canada. *Geology* 30, 391–394.
- MAJOR, R.B. & TELUK, J.A., 1967. The Kulyong Volcanics. *Geological Survey of South Australia Quarterly Geology Notes* 22, 8–11.
- MÁNGANO, M.G., BUATOIS, L.A. & ACEÑOLAZA, G.F., 1996. Trace fossils and sedimentary facies from a Late Cambrian–Early Ordovician tide-dominated shelf (Santa Rosita Formation, northwest Argentina): implications for ichnofacies models of shallow marine successions. *Ichnos* 5, 53–88.
- MANTON, S.M., 1977. *The Arthropoda*. Clarendon Press, Oxford, 527 pp.
- MAPLES, C.G. & ARCHER, A., 1989. The potential of Paleozoic non-marine trace fossils for paleoecological interpretations. *Palaeogeography Palaeoclimatology Palaeoecology* 73, 185–195.
- MAPSTONE, N.B. & MCLROY, D., 2006. Ediacaran fossil preservation: taphonomy and diagenesis of a discoid biota from the Amadeus Basin, central Australia. *Precambrian Research* 149, 129–148.
- MARTINSSON, A., 1970. Toponymy of trace fossils. *Geological Journal Special Issue* 3, 323–330.
- MCLROY, D., CRIMES, T.P. & PAULEY, J.C., 2005. Fossils and matgrounds from the Neoproterozoic Longmyndian Supergroup, Shropshire, UK. *Geological Magazine* 142, 441–455.
- McNAMARA, K.J. & TREWIN, N.H., 1993. A euthycarcinoid arthropod from the Silurian of Western Australia. *Palaeontology* 36, 319–335.
- MCNEILL, J. (and 11 others), 2006. International Code of Botanical Nomenclature (Vienna Code) adopted by the seventeenth International Botanical Congress, Vienna, Austria. A.R.G. Ganter Verlag, Ruggell, Liechtenstein, 568 pp.
- MIKULÁŠ, R., 1994. Trace fossils at the Arenig–Llanvirn boundary (Ordovician, Czech Republic). *Czech Geological Society Journal* 39, 205–212.

- MIKULÁS, R., 1995. Trace fossils from the Paseky Shale (Early Cambrian, Czech Republic). *Czech Geological Society Journal* 40, 37–44.
- MOORE, P.S., 1990. Origin of redbeds and variegated sediments, Cambrian, Adelaide Geosyncline, South Australia. *Geological Society of Australia Special Publication* 16, 334–350.
- MORRISSEY, L.B. & BRADY, S.J., 2004. Terrestrial trace fossils from the Lower Old Red Sandstone, south-west Wales. *Geological Journal* 39, 315–336.
- MORRISSEY, L.B., BRADY, S.J., BENNETT, J.P., MARRIOTT, S.B. & TARRANT, P.R., 2004. Fish trails from the Lower Old Red Sandstone at Tredomen Quarry, Powys, southeast Wales. *Geological Journal* 29, 337–358.
- MYROW, P.M., 1995. *Thalassinoides* and the enigma of early Paleozoic open-framework burrow systems. *Palaios* 10, 58–74.
- NARBONNE, G.M., SAYLOR, B.Z. & GROTZINGER, J.G., 1997. The youngest Ediacaran fossils from southern Africa. *Journal of Paleontology* 71, 953–967.
- NEEF, G., 2004a. Devonian arthropod trackways from the fluvial Ravensdale Formation, western New South Wales. *Alcheringa* 28, 401–402.
- NEEF, G., 2004b. Non-marine (?Late Silurian–Early Devonian) trace fossils, Darling Basin, western New South Wales. *Alcheringa* 28, 389–399.
- NICHOLSON, H.A., 1873. Contributions to the study of the errant annelides of the older Palaeozoic rocks. *Royal Society of London Proceedings* 21, 288–290.
- NOFFKE, N., GERDES, G., KLENKE, T. & KRUMBEIN, W.E., 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, W.E., 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 Archean tidal flats (3.2 Ga Moodies Group, South Africa). *Geology* 34, 253–256.
- OLSEN, H., DUE, P.H. & CLEMMENSEN, L.B., 1989. Morphology and genesis of asymmetric adhesion warts: a new adhesion surface structure. *Sedimentary Geology* 61, 277–285.
- PATERSON, J.R. & BROCK, G.A., 2007. Early Cambrian trilobites from Angorichina, Flinders Ranges, South Australia, with a new assemblage from the *Pararaia bunyeroensis* Zone. *Journal of Paleontology* 81, 116–142.
- PEMBERTON, S.G. & FREY, R.W., 1982. Trace fossil nomenclature and the *Planolites-Palaeophycus* dilemma. *Journal of Paleontology* 56, 843–861.
- PICKERILL, R.K., ROMANO, M. & MELENDEZ, B., 1984. Arenig trace fossils from the Salamanca area, western Spain. *Geological Journal* 19, 249–269.
- POIRÉ, D.G., SPALLETTI, L.A. & DEL VALLE, A., 2003. The Cambrian–Ordovician siliciclastic platform of the Balcarce Formation (Tandilia System), Argentina: facies, trace fossils, paleoenvironments and sequence stratigraphy. *Geologica Acta* 1, 41–60.
- PRAVE, A.R., 2002. Life on land in the Proterozoic: evidence from the Torridonian rocks of Northwest Scotland. *Geology* 30, 811–814.
- REMY, W., REMY, R., HASS, H., SCHULTKA, S. & FRANZMEYER, F., 1980. *Sciadophyton* Steinmann—ein gametophyt aus dem Siegen. *Argumenta Palaeobotanica* 6, 73–94.
- REMY, W., GENSEL, P.G. & HASS, H., 1993. The gametophyte generation of some Early Devonian land plants. *International Journal of Plant Science* 154, 35–58.
- RESTALLACK, G.J., 1992. What to call early plant formations on land. *Palaios* 7, 508–520.
- RESTALLACK, G.J., 1994. Were the Ediacaran fossils lichens? *Paleobiology* 20, 523–544.
- RESTALLACK, G.J., 1997. *A Colour Guide to Paleosols*. John Wiley, Chichester, 175 pp.
- RESTALLACK, G.J., 1998. Fossil soils and completeness of the rock and fossil records. In *The Adequacy of the Fossil Record*, S.K. DONOVAN & C.R.C. PAUL, eds, John Wiley, Chichester, 133–163.
- RESTALLACK, G.J., 2000. Ordovician life on land and early Paleozoic global change. In *Phanerozoic Terrestrial Ecosystems*, R.A. GASTALDO & W.A. DiMICHELE, eds, Paleontological Society Papers 6, 21–45.
- RESTALLACK, G.J., 2001. *Scoyenia* burrows from Ordovician paleosols of the Juniata Formation in Pennsylvania. *Palaontology* 44, 209–235.
- RESTALLACK, G.J., 2005. Pedogenic carbonate proxies for amount and seasonality of precipitation in paleosols. *Geology* 33, 333–336.
- RESTALLACK, G.J., 2007. Growth, decay and burial compaction of *Dickinsonia*, an iconic Ediacaran fossil. *Alcheringa* 31, 215–240.
- RESTALLACK, G.J., 2008. Cambrian paleosols and landscapes of South Australia. *Australian Journal of Earth Science* 55, 1083–1106.
- RESTALLACK, G.J., 2009. Cambrian, Ordovician and Silurian pedostratigraphy and global events in Australia. *Australian Journal of Earth Sciences* 56, 571–586.
- RICHTER, R., 1937. Marken und Spuren aus allen Zeiten. I–II. *Senckenbergiana* 19, 150–169.
- RIDE, W.D.L., COGGER, H.G., DUPUIS, C. *et al.*, (eds), 1999. *International Code of Zoological Nomenclature*. International Trust for Zoological Nomenclature, London, 306 pp.
- ROBISON, R.A., 1990. Earliest known uniramous arthropod. *Nature* 343, 163–164.

- ROMANO, M. & WHYTE, M.A., 1987. A limulid trace fossil from the Scarborough Formation (Jurassic) of Yorkshire: its occurrence, taxonomy and interpretation. *Yorkshire Geological Society Proceedings* 46, 85–95.
- ROMANO, M. & WHYTE, M.A., 1990. *Selenichnites*, a new name for the ichnogenus *Selenichnus* Romano and Whyte, 1987. *Yorkshire Geological Society Proceedings* 48, 221.
- ROSE, E.C., 2006. Non-marine aspects of the Cambrian Tonto Group of the Grand Canyon, USA, and broader implications. *Palaeoworld* 15, 223–241.
- RUNNEGAR, B.N. & FEDONKIN, M.A., 1991. Proterozoic metazoan body plans. In *The Proterozoic Biosphere: a Multidisciplinary Study*, J.W. SCHOPF & C. KLEIN, eds, Cambridge University Press, Cambridge, 369–388.
- SAPORTA, G. & MARION, A.F., 1883. *Die Paläontologische Entwicklung des Pflanzenreichs: die Kryptogamen*. F.A. Brockhaus, Leipzig, 250 pp.
- SCHRAM, F.R. & ROLFE, W.D.I., 1982. New euthycarcinoid arthropods from the Upper Pennsylvanian of France and Illinois. *Journal of Paleontology* 56, 1434–1450.
- SEILACHER, A., 1955. Spuren und Lebenweise der Trilobiten: Spuren und Fazies im Unterkambrium. *Akademie der Wissenschaften und der Literatur im Main Abhandlungen Mathematische-Naturwissenschaftliche Klasse* 10, 86–143.
- SEILACHER, A., 1992. Vendobionta and Psammocorallia: lost constructions of Precambrian evolution. *Geological Society of London Journal* 149, 607–613.
- SEILACHER, A., 2007. *Trace Fossil Analysis*. Springer, London, 226 pp.
- SEILACHER, A., 2008. Biomats, biofilms, and biogluce as preservational agents for arthropod trackways. *Palaeogeography Palaeoclimatology Paleocology* 270, 252–257.
- SEWARD, A.C., 1894. *Catalogue of the Mesozoic Plants in the Department of Geology, British Museum. The Wealden Flora Pt 1*. British Museum (Natural History), London, 252 pp.
- SHANKER, R., MATHUR, V.K., KUMAR, G. & SRIVASTAVA, M.C., 1997. Additional Ediacaran biota from the Krol Group, lesser Himalaya, India, and their significance. *Geoscience Journal* 18, 79–94.
- SHAUB, B.M., 1939. The origin of stylolites. *Journal of Sedimentary Petrology* 9, 47–61.
- SMITH, A.J.E., 1990. *The Liverworts of Britain and Ireland*. Cambridge University Press, Cambridge, 362 pp.
- SPERLING, E., VINTHER, J., BRIGGS, D.E.G., PISANI, D. & PETERSON, K.J., 2008. A placozoan affinity for *Dickinsonia* and the evolution of Late Precambrian feeding modes. *Geological Society of America Abstracts* 40(6), 316–6.
- SPRIGG, R.E., 1947. Early Cambrian (?) jellyfishes from the Flinders Ranges, South Australia. *Royal Society of South Australia Transactions* 71, 212–224.
- STEINER, M. & REITNER, J., 2001. Evidence of organic structures in Ediacara-type fossils and associated microbial mats. *Geology* 29, 1119–1122.
- STEVENS, M.K. & APAK, S.N., 1999. Empress 1 and 1A well completion report, Yowalga Sub-basin, Officer Basin, Western Australia. *Geological Survey of Western Australia Report* 4, 1–20.
- STOCK, E.C., 1974. The clay mineralogy, petrology and environments of deposition of the Cambrian Lake Frome Group, Flinders Ranges, South Australia. Unpublished MSc thesis, Department of Geology, University of Adelaide, 188 pp.
- STROTHER, P. K., 2000. Cryptospores: the origin and early evolution of the terrestrial flora. In *Phanerozoic Terrestrial Ecosystems*, R.A. GASTALDO & W.A. DiMICHELE, eds, Paleontological Society Special Papers 6, 3–17.
- SUN, W., 1986. Medusae from the uppermost Precambrian or Cambrian sandstones, central Australia. *Palaeontology* 31, 325–360.
- TAYLOR, T.N., KLAVINS, S.D., KRINGS, M., TAYLOR, E.L., 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, A.M.F. & ROTHWELL, G.W., 2006. Wetlands before tracheophytes: thalloid terrestrial communities of the Early Silurian Passage Creek biota (Virginia). In *Wetlands Through Time*, S.F. GREB & W.A. DiMICHELE, eds, Geological Society of America Special Paper 399, 41–56.
- TREWIN, N.H. & McNAMARA, K.J., 1994. Arthropods invade the land; trace fossils and paleoenvironments of the Tumblogooda Sandstone (?late Silurian) of Kalbarri, Western Australia. *Royal Society of Edinburgh Earth Sciences Transactions* 85, 177–210.
- TUCKER, M.D., 1991. Carbon isotopes and Cambrian–Precambrian boundary geology South Australia: ocean basin formation, seawater chemistry and organic evolution. *Terra Nova* 1, 573–582.
- VACCARI, N.E., EDGEcombe, G.D. & ESCUDERO, C., 2004. Cambrian origins and affinities of an enigmatic fossil group of arthropods. *Nature* 430, 554–557.
- VANGUESTAINE, M. & BRUECK, P., 2005. A Middle Cambrian age for the Ediacara-type fauna from the Booley Bay Formation, County Wexford, Ireland; new acritarch data and their implications. *Carnets de Geologie M02*, 61–62.
- WALCOTT, C.D., 1914. Cambrian geology and paleontology. III(2). Pre-Cambrian algal flora. *Smithsonian Miscellaneous Collections* 64, 77–156.
- WALTON, J., 1923. On a new method of investigating fossil plant impressions or incrustations. *Annals of Botany* 37, 379–391.

- WEAVER, P.G., MCMENAMIN, M.A.S. & TACKER, R.C., 2006. Paleoenvironmental and paleobiogeographic implications of a new Ediacaran body fossil from the Neoproterozoic Carolina Terrane, Stanly County, North Carolina. *Precambrian Research* 150, 123–135.
- WEBBY, B.D., 1970. Late Precambrian trace fossils from New South Wales. *Lethaia* 3, 79–109.
- WEBER, B. & BRADY, S.J., 2004. A marginal marine ichnofauna from the Blaiklock Group (?Lower Ordovician) of the Shackleton Range, Antarctica. *Royal Society of Edinburgh Earth Sciences Transactions* 94, 1–20.
- WHITE, C.D., 1929. Flora of the Hermit Shale, Grand Canyon, Arizona. *Carnegie Institution of Washington Publication* 405, 221 pp.
- WILLIAMS, G.E. & SCHMIDT, P.W., 2003. Possible fossil impression from the late Palaeoproterozoic–early Mesoproterozoic Semri Group (lower Vindhyan Supergroup), central India. *Alcheringa* 27, 75–76.
- WRIGHT, J.L., QUINN, L., BRIGGS, D.E.G. & WILLIAMS, S.H., 1995. A subaerial arthropod trackway from the Upper Silurian Clam Bank Formation of Newfoundland. *Canadian Journal of Earth Sciences* 32, 304–313.
- YUAN, X.-L., XIAO, S.-H. & TAYLOR, T.N., 2005. Lichen-like symbiosis 600 million years ago. *Science* 308, 1017–1020.