Alcheringa: An Australasian Journal of Palaeontology

Growth, decay and burial compaction of **Dickinsonia**, an iconic Ediacaran fossil

PLEASE SCROLL DOWN FOR ARTICLE

Growth, decay and burial compaction of *Dickinsonia*, an iconic Ediacaran fossil

GREGORY J. RETALLACK

Dickinsonia is a Neoproterozoic, Ediacaran fossil, variously considered a polychaete, turbellarian or annelid worm, jellyfish, polyp, xenophyophoran protist, lichen or mushroom. Its preservation as unskeletonized impressions in quartz sandstones has been attributed to a Neoproterozoic regime of aerobic decay less effective than today, microbial pyritization much nearer the surface than today, or agglutinate-mineralization as in xenophyophorans. However, the great variation in thickness independent of width or length of South Australian *Dickinsonia* is evidence of decay like the wilting of a fossil leaf, lichen or mushroom, but unlike clotting and distortion during decay, wilting or osmotic shrinkage of modern and fossil worms and jellyfish. Decayed specimens of *Dickinsonia* arrayed in arcs have been interpreted as slime trails or tumble tracks, but can also be interpreted as rhizinous bases of decayed crustose lichens or mushrooms arranged in fairy rings. *Dickinsonia* is interpreted to be sessile because adjacent specimens show reaction rims indicative of competitive interaction, and because no overlapping well-preserved specimens have ever been found. Folded and bent *Dickinsonia* reveal firm attachment and limited flexibility, but no brittle deformation indicative of pyritic, sideritic or calcitic 'death masks' or xenophyophoran agglutinate skeletons. *Dickinsonia* was resistant to compaction by overburden, like fossil lichens such as *Spongiophyton* and *Thucomyces*, and more compaction-resistant than fossil logs, jellyfish or worms. *Dickinsonia* also shows indeterminate growth like lichens, fungi, plants, xenophyophorans and colonial animals. Growth, decay and burial compaction of *Dickinsonia* were more like those of plants, lichens and fungi, than of worms, jellyfishes or anemones.

G.J. Retallack [gregr@uoregon.edu], Department of Geological Sciences, University of Oregon. Eugene, OR 97403-1272, USA; received 18.11.05, revised 23.3.06.

DICKINSONIA is an iconic Ediacaran fossil, best known from Neoproterozoic sandstones of South Australia (Jenkins *et al*. 1983, Jenkins 1992), and Russia (Fedonkin 1992, Grazhdankin 2004), and perhaps China (Niu & Shu 2000). It was the giant of its age, reaching 1.4 m in length (Jenkins 1996). *Dickinsonia* has a striking regularity of symmetrically disposed segments (Fig. 1A), unlike other unskeletonized, irregularly circular and elongate Ediacaran fossils (Glaessner 1984). A variety of other fossils such as *Andiva* and *Vendia* show similarities with *Dickinsonia* (Fedonkin 2002), but only *Dickinsonia* is considered here. This paper presents new measurements of

width, length and depth of *Dickinsonia* from the Ediacara Hills and Brachina Gorge, South Australia as tests of three fundamental questions about these enigmatic fossils. What kind of organism were they? Did they decay? How were they preserved?

Biological affinities of *Dickinsonia* remain problematic. At first *Dickinsonia* was considered a jellyfish (Sprigg 1947), and assigned to an order Dipleurozoa distinguished by bilateral symmetry found in no other jellyfish (Harrington & Moore 1956). Comparison with the tiny parasitic polychaete worm *Spinther* (Wade 1972), and interpretations as an extinct annelid worm (Conway Morris 1979) or turbellarian flatworm (Termier & Termier 1968, Fedonkin 1981) have had the greatest sway (Runnegar 1982, Gehling 1991, Jenkins 1996), despite
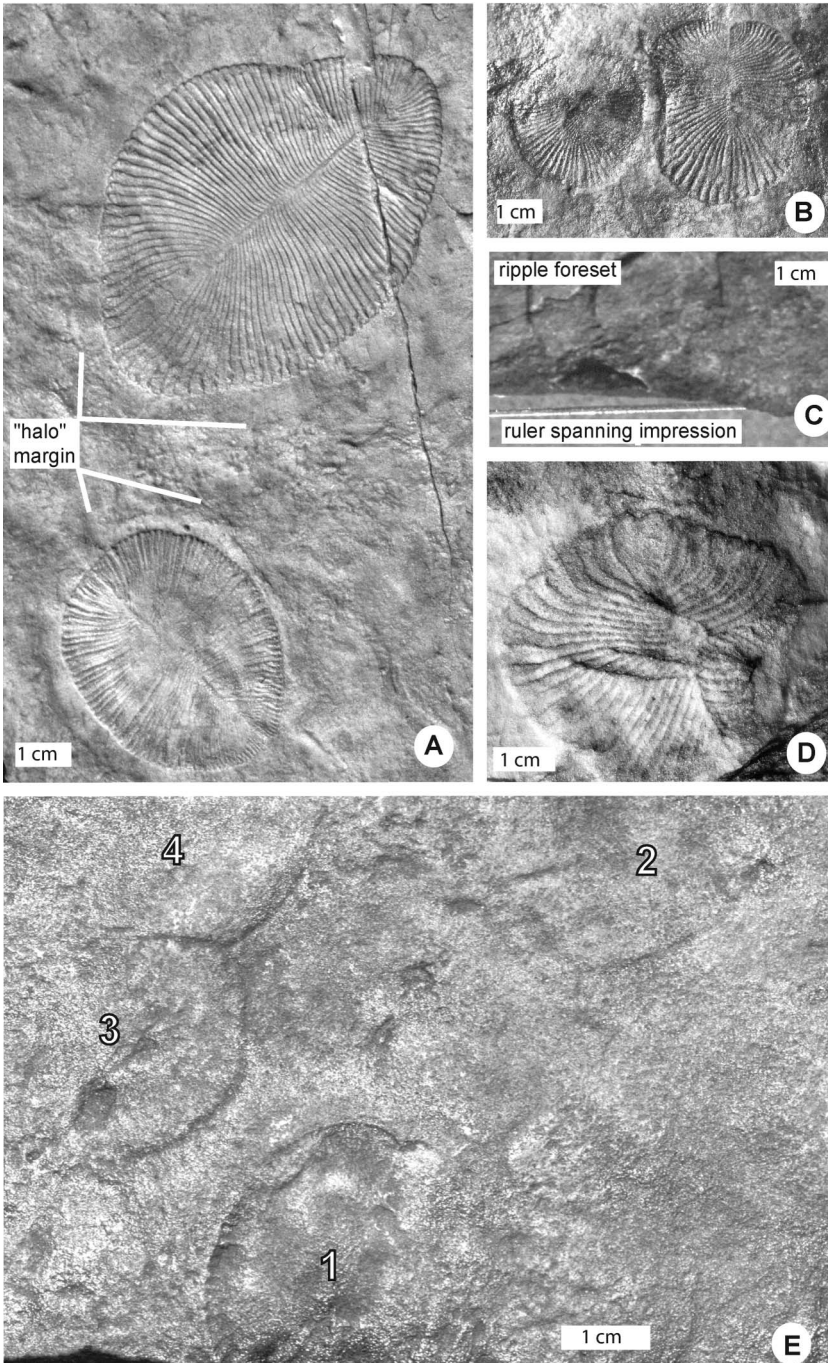
Fig. 1. Dickinsonia costata (**A** upper, **B–E**) and *D. tenuis* (**A** lower only) from the late Precambrian Ediacara Member of the Rawnsley Quartzite in the Ediacara Hills (**A–B**, **D–E**) and Brachina Gorge (**C**), showing marginal haloes (**A**), likely competitive interaction (**B**), undeformed overlying ripple mark (**C**), wrinkling and folding (**D**), and different degrees of decay (**E**). Scale bars are all 1 cm; specimens are located in the South Australian Museum (A = F17462, B = F13760, D = F13977, E = F14359) and Condon Museum, University of Oregon (C = F34285).

Dickinsonia's mattress-like construction (Seilacher 1989). *Dickinsonia* also has similarities with xenophyophoran protists of the deep sea (Zhuravlev 1993, Seilacher *et al.* 2005), although 1.4 m is unusually large for a single cell of this kind, and there is no physicochemical trace of the mineralized-agglutinate skeleton found in such giant protists (Tendal 1972). The scleractinian coral *Fungia*, so-named for its resemblance to mushrooms, also has superficial similarity to *Dickinsonia* (Valentine 1992). There is no trace of calcareous coralline skeletonization in *Dickinsonia*, and if it were a comparable polyp or anemone, its mesenteric structure is bilaterally symmetrical rather than the usual cnidarian radial symmetry. *Dickinsonia* has also been interpreted as a mushroom or lichenized fungus or actinobacterium (Retallack 1994, 1995), but is strikingly regular compared, for example, with ridged crustose lichens, which are often necrosed or grazed in older parts of the thallus (Brodo *et al.* 2001). There has been gathering evidence for generally microbial (Steiner & Reitner 2001, Grazhdankin & Seilacher 2002, Seilacher *et al.* 2003), and for specifically fungal (Peterson *et al.* 2003) or lichen (Yuan *et al.* 2005) affinities of Ediacaran fossils. *Dickinsonia* also has been placed in the extinct phyla Vendozoa or Vendobionta (Seilacher 1992, Seilacher *et al.* 2003) or extinct triploblastic-metazoan phylum Proarticulata (Fedonkin 2003). My measurements of size variation in *Dickinsonia* test these various hypotheses by evaluating modes of growth.

The issue of decay in Ediacaran fossils was raised by Seilacher (1989) as a solution for the preservation of unskeletonized fossils in red, non-carbonaceous, quartz sandstones, which do not preserve soft-bodied fossils at other times in Earth history. He proposed that Ediacaran fossils were preserved because Neoproterozoic decay was less effective than it is today. My measurements of impression depth test the hypothesis of decay, which should be revealed by varying depth and clarity of impressions, vs decay retardation, which should reveal consistent depth and clarity of impressions.

The preserved resistance to burial compaction of Ediacaran fossils has long been perceived as anomalous: see, for example, Wade (1968), who postulated cementation before or shortly after burial, comparable with iron oxide encrustation of leaves in ponds (Spicer 1977). Another possibility is preservation as 'death masks' mineralized by pyrite within shallowly buried (1–2 cm) microbial mats (Gehling 1999). Yet another view is that *Dickinsonia* had some kind of tough biopolymer, comparable with lignin of wood or chitin of lichens (Retallack 1994), perhaps a coherent biopolymer carapace (Fedonkin 2002). Cements or mineral skeletons are little compacted by burial compared with wood (Retallack 1994), but now *Dickinsonia* can be compared for the first time with burial compaction of newly recognized fossil fungi and lichens (Jurina & Krassilov 2002), including Devonian *Spongiophyton* (Stein *et al.*1993, Retallack 1994, Jahren *et al.* 2003), Siluro-Devonian *Prototaxites* (Hueber 2001), and Archaean *Thucomyces* (Hallbauer & Van Warmelo 1974, Hallbauer *et al.* 1977, MacRae 1999). Although Cloud (1976) considered *Thucomyces* to be an artefact of acid maceration, *Thucomyces* is known within thin-sections and slabs, where it is cut by veins of metamorphic chlorite and quartz (MacRae 1999). The range of carbon isotopic composition of *Spongiophyton minutissimum* also indicates that they were lichens (Jahren *et al.* 2003), even if absolute values are undiagnostic (Fletcher *et al.* 2004). Additional measurements of the compaction resistance of wood are presented here, together with new measurements of the compaction resistance of fossil lichens, for comparison with measurements of resistance to burial of *Dickinsonia*.

Materials and methods

This study is based on examination of type collections of *Dickinsonia* from the Ediacara Hills and Flinders Ranges, South Australia, in the South Australian Museum and Department of Geology and Geophysics of the University of Adelaide, and two specimens from Brachina Gorge, Flinders Ranges, South Australia, in the Condon Collection, University of Oregon (Retallack 1994). This study follows the classification of Jenkins (1992) who recognized four species: *Dickinsonia costata* Sprigg, 1947 (by far the most common), *D. tenuis* Glaessner & Wade, 1966, *D. rex* Jenkins, 1992 (both uncommon) and *D. lissa* Wade, 1972 (rare). The width and length of all specimens were measured with a Vernier micrometer accurate to 0.1 mm, and the depth of the impression was measured with a Vernier depth gauge accurate to 0.025 mm (Table 1). A Vernier depth gauge is a high-precision instrument designed for automotive engineers to determine the degree of flatness of a surface. It measures protrusion of a piston 3 mm in diameter from a planar surface 10×1 cm, so picks out general levels rather than details of ribbing in *Dickinsonia*.

This paper extends previous isotaphonomic studies (Retallack 1994, 1995) measuring the thickness and width of fossil log compressions in quartz sandstones (Tables 2–3), because logs are compressed in thickness but not width (Rex & Chaloner 1983) and are commonly preserved in quartz sandstones like Ediacaran fossils. Depth of burial was derived from geological estimates of overburden (Table 3), supported by point counting the number of neighbouring grains per grain (Taylor 1950). Depths of burial for previously studied fossil logs (Retallack 1994, 1995) from North America have been estimated from thermo-mechanical modelling of Beaumont et al. (1988) as 7.8 km (Big Savage Mountain), 3.6 km (Sugar Creek Mountain), and 3.3 km (Cabin Creek and Bragg Corner). Unlike previously studied fossil logs chosen for matrix and burial depth close to maximal likely burial of Ediacaran fossils (Retallack 1994, 1995), the fossil logs studied here were chosen to explore a wider range of burial depth and petrographic variation within quartz sandstones (Fig. 2). These new data thus include shallow depths of burial for Ediacaran fossils (400–1500 m) advocated by Gehling (1999).

Also compared with preservation of *Dickinsonia* are fossil fungi and lichens discovered or confirmed within the last decade (MacRae 1999, Hueber 2001, Jahren et al. 2003). Burial compaction of fossil fungi and lichens was estimated (Table 4) from the flattening of tubular hyphae in SEM photomicrographs (Chaloner et al. 1974, Hallbauer et al. 1977, Strother 1988, Gensel et al. 1991), because the tubes are circular in cross-section within permineralized specimens (Hallbauer et al. 1977, Hueber 2001).

Affinities indicated by width and length measurements

Dickinsonia specimens range from 4 to 1400 mm long (Wade 1972, Jenkins 1996). South Australian collections appear to be a remarkably complete growth series (Runnegar 1982, Retallack 1994), with individuals of different size on the same bedding planes (Fig. 1A). This in itself is evidence for preservation where they lived, and the following paragraphs further justify this necessary assumption of growth-series analysis.

The preservational habitats of *Dickinsonia* can be inferred from enclosing ripple-marked and mud-cracked, red shales and flaggy white sandstones. Red Neoproterozoic and Cambrian shales of South Australia were originally red or brown, and not reddened by later soil formation for the

following reasons. The Ediacara Member is red in boreholes to depths of 91 m below the surface (Goldring & Curnow 1967). Clasts of shale in intraformational breccia are red. Red pigment is a diffuse stain radiating from iron-rich minerals (Moore 1990). Hematite cements pass palaeomagnetic fold tests in soft-sediment deformation and are consistent with other indications of late Precambrian palaeopoles (Schmidt *et al*. 1993). The flaggy sandstones also have red clasts, but are mostly white and unusually clean of organic matter, with well-sorted, and well-rounded grains, almost entirely of quartz, indicating well-oxidized water and slow accumulation along a tectonically inactive coast (Jenkins 1996). Further evidence of oxidizing and periodically exposed palaeoenvironments come from microbial mat deformation and cracking like that found in sulfate evaporites (Gehling 1999). The red beds were most likely laid down in tidal flats and floodplains, and the flaggy sandstones were probably deposited in estuarine palaeochannels and shallow subtidal shorefaces (Jenkins *et al*. 1983, Jenkins 1996). *Dickinsonia* impressions are common on the soles of the flaggy sandstones (Retallack 1994).

Dickinsonia was probably a sessile organism of estuarine to subtidal environments and preserved autochthonously based on the following observations. Even in tidal flat facies with abundant elephant-skin-texture of microbial mats, *Dickinsonia* specimens vary in size, unlike stranded schools of jellyfish of very uniform size range thrown up on beaches and mudflats by storms (Norris 1989, Retallack 1994, Hagadorn *et al*. 2002). No well-preserved *Dickinsonia* is known to overlap another clearly preserved *Dickinsonia*, or any other clearly preserved fossil (Gehling *et al*. 2005). A specimen illustrated here (Fig. 1B) shows the closest known pair of *Dickinsonia* specimens. The right-hand specimen has a thickened reaction rim to the encroachment of

the left-hand specimen, similar to allelopathic competitive interaction between adjacent corals and sponges (Jackson & Buss 1975), encrusting bryozoans (Kidwell & Gyllenhaal 1998), and crustose lichens (Brodo *et al*. 2001). The rims are not in contact, nor buckled, nor shuffled against one another, as would be the case for stacking of unattached corpses. Flume experiments have shown that *Dickinsonia* must have been firmly attached to the substrate in order to be preserved at the base of crossbeds (Schopf & Baumiller 1998). Dismembered specimens of *Dickinsonia* (Gehling *et al*. 2005, fig. 9) show extensive disruption of sediment, apparently attached. A mudcrack through one *Dickinsonia* has separated two undeformed halves by 2–9 mm (South Australian Museum specimen P41164). Ediacaran slabs show a marked absence of tool marks, size sorting or other evidence of transport of fossils (Gehling *et al*. 2005). Analysis of growth series is not appropriate for fossils that have been transported and sorted during deposition, but *Dickinsonia* appears to have been sessile, firmly attached, and in place of growth.

The specimens of *Dickinsonia* casually collected over many years largely from a single site in the Ediacara Hills are unlikely to represent a single population, but are the largest available suite of samples. Collections of individual populations from single bedding planes are becoming available (Droser *et al*. 2003), but not yet as numerous as the results presented here (Table 1).

Growth in width and length show two linear arrays though the origin, here interpreted as two distinct species: (1) *Dickinsonia costata*, with wide segments, narrow midrib, and oval shape, and (2) *D. tenuis*, with narrow segments, wide midrib, and elongate shape (Fig. 3A). A widely illustrated specimen (Fig. 1A) is here interpreted as a co-occurrence of these two species, rather than a contracted and expanded example of the same species of

Number	Length (mm)	Width (mm)	Depth (mm)	Height (mm)	Taxon
CCF34285	Incomplete	161	4.000		*Dickinsonia costata*
CCF34288	Incomplete	44.9	2.600		*Dickinsonia costata*
F17462-4	132.8	95.9	2.210		*Dickinsonia costata*
F17462-4	77.9	63.7	3.505		*Dickinsonia tenuis*
MW1275/1	78.5	64.7	1.626		*Dickinsonia costata*
MW165a,b	Incomplete	61.2	1.702	1.2	*Dickinsonia costata*
MW168	60.6	35.5	1.626		*Dickinsonia costata*
MW187	46.2	34.6	0.660		*Dickinsonia costata*
MW189	55.1	41.5	0.864		*Dickinsonia costata*
MW196	8.7	8.2	0.203		*Dickinsonia costata*
MW199	68.2	50.8	0.838		*Dickinsonia costata*
MW204	25.1	21.7	1.194		*Dickinsonia costata*
MW205	Incomplete	18.8	0.940		*Dickinsonia costata*
MW299	169.7	147.9	2.642		*Dickinsonia costata*
MW553	Incomplete	54.5	1.549		*Dickinsonia costata*
MW554	51.6	64.7	0.279		*Dickinsonia costata*
MW556	74.3	61.8	2.591		*Dickinsonia costata*
MW557	34.2	23.9	1.422		*Dickinsonia costata*
MW558	Incomplete	32.6	1.905		*Dickinsonia costata*
MW559	50.6	31.3	0.838		*Dickinsonia costata*
MW561	Incomplete	81.4	2.057		*Dickinsonia costata*
MW563	37.5	28.5	1.753		*Dickinsonia costata*
MW741a,b	Incomplete	36.7	1.600	0.9	*Dickinsonia costata*
P12557	65.9	61.6	1.372		*Dickinsonia costata*
P12678	38.5	42.4	1.600		*Dickinsonia costata*
P12690	33.7	25.7	1.626		*Dickinsonia costata*
P12724	55.8	45.5	2.007		*Dickinsonia costata*
P12725	33.7	25.1	2.311		*Dickinsonia costata*
P12727	Incomplete	41.7	0.330		*Dickinsonia costata*
P12728	99.5	72.6	2.311		*Dickinsonia costata*
P12729	72.3	63.5	2.261		*Dickinsonia costata*
P12749	63.3	61.3	0.737		*Dickinsonia costata*
P12900	38.5	28.1	0.584		*Dickinsonia costata*
P13718	30.7	21.7	1.626		*Dickinsonia costata*
P13760	37.3	36.9	0.965		*Dickinsonia costata*
P13760	48.7	41.3	0.305		*Dickinsonia costata*
P13767	165.9		1.753		*Dickinsonia costata*
P13799	43.5	44.5	2.515		*Dickinsonia costata*
P14221	21.5	17.6	0.152		*Dickinsonia costata*
P14241	53.3	53.8	1.676		*Dickinsonia costata*
P14322	89.6	59.7	1.676		*Dickinsonia costata*
P14327	208.6	140.8	2.261		*Dickinsonia tenuis*
P14328	61.9	49.8	2.235		*Dickinsonia costata*
P14330	22.5	22.8	1.346		*Dickinsonia costata*
P14331	17.9	19.3	0.356		*Dickinsonia costata*
P14333	Incomplete	106.7	1.600		*Dickinsonia rex*
P14334	323.8	193.7	4.140		*Dickinsonia rex*
P14342	Incomplete	56.7	2.210		*Dickinsonia tenuis*
P14344	18.7	16.5	0.991		*Dickinsonia costata*
P14350	83.7	71.5	0.737		*Dickinsonia costata*

Table 1. Measurements of *Dickinsonia* fossils from South Australia.   (*continued*)

Table 1. (*Continued*).

Number	Length (mm)	Width (mm)	Depth (mm)	Height (mm)	Taxon
P14351	14.3	13.9	0.991		*Dickinsonia costata*
P14352	13.3	12.5	0.737		*Dickinsonia costata*
P14352	65.5	56.7	2.210		*Dickinsonia tenuis*
P14353	59.5	42.7	0.178		*Dickinsonia costata*
P14354	11.2	10.8	0.254		*Dickinsonia costata*
P14354	177.5	160.7	4.674		*Dickinsonia costata*
P14355	28.3	22.8	0.330		*Dickinsonia costata*
P14359	43.9	33.9	0.711		*Dickinsonia costata*
P14360	21.8	19.3	1.981		*Dickinsonia costata*
P14360	21.5	22.2	0.965		*Dickinsonia costata*
P14361	26.2	24.7	0.356		*Dickinsonia costata*
P14364	34.7	31.7	0.457		*Dickinsonia costata*
P14365a	29.1	20.5	0.381		*Dickinsonia costata*
P14365b	34.8	26.9	0.279		*Dickinsonia costata*
P14366	43.9	36.8	1.778		*Dickinsonia costata*
P14367a	62.3	45.7	1.295		*Dickinsonia costata*
P14368	19.2	21.9	1.295		*Dickinsonia costata*
P14369	Incomplete	40.2	1.321		*Dickinsonia costata*
P14370	44.5	40.2	1.981		*Dickinsonia costata*
P14372	47.9	36.7	1.499		*Dickinsonia costata*
P14373	57.8	42.7	2.311		*Dickinsonia costata*
P14377	59.3	55.1	0.152		*Dickinsonia costata*
P14378	54.6	38.6	0.432		*Dickinsonia costata*
P14379	59.9	52.8	0.457		*Dickinsonia costata*
P14389	28.7	23.9	0.889		*Dickinsonia costata*
P14393	125.8	100.1	2.311		*Dickinsonia costata*
P14395	45.9	43.2	1.295		*Dickinsonia costata*
P17998	160.2	81.7	4.013		*Dickinsonia tenuis*
P18888	41.4	25.7	2.464		*Dickinsonia tenuis*
P21155	49.1	34.5	0.457		*Dickinsonia tenuis*
T45;1005	35.5	25.5	1.397		*Dickinsonia costata*
T45;2001	95.9	65.8	2.007		*Dickinsonia costata*
T46;2009	60.8	60.6	1.600		*Dickinsonia costata*
T47;2052	50.8	45.5	0.991		*Dickinsonia tenuis*
T50;2001	30.2	23.8	0.305		*Dickinsonia tenuis*
T51;2000	68.5	58.8	1.397		*Dickinsonia tenuis*
T53;2004	101.9	87.5	2.159		*Dickinsonia costata*
T54;2050	Incomplete	82.6	2.896		*Dickinsonia rex*
T60;2054	40.1	32.2	0.305		*Dickinsonia costata*
T61;2061	55.6	49.9	1.118		*Dickinsonia costata*
Unnumbered	35.8	35.2	1.549	0.9	*Dickinsonia costata*
Unnumbered	62.3	65.3	1.473		*Dickinsonia costata*
Unnumbered	91.7	80.3	1.295		*Dickinsonia costata*
Unnumbered	Incomplete	131.7	4.674		*Dickinsonia rex*

Note: This includes collections by Mary Wade (MW-) in the Geology Department of Adelaide University, and by Reginald Sprigg (T-), and bulk collections (P-, F-) in the South Australian Museum, and two specimens (CCF-) in the Condon Collection, University of Oregon. Length is dimension of long axis and width dimension of short axis, whereas depth is distance below surface of concave impression and height is the distance from the surface of the convex counterpart (this latter known only in two specimens). Taxonomy is after Jenkins (1992).

Locality number	Locality description	Formation	Age	References
L2998	Portal Mountain, Antarctica: 34.3 m above lower dolerite on eastern spur: S78.11007° E159.39183°	Weller Coal Measures	mid-Permian	Collinson *et al.* (1994)
L3000	Parramatta, New South Wales, Australia: on track above creek in northern part of The Kings School: S33.78392° E151.01289°	Hawkesbury Sandstone	Middle Triassic	Conaghan (1980), Herbert (1980), Crawford *et al.* (1980)
L3001	Axhandle Canyon, Utah, USA: 118.7 m stratigraphically above the base of the northeast ridge at the canyon mouth: N39.40268° W111.68204°	North Horn Formation	Paleocene	Hintze (1988), Talling *et al.* (1994)
L3002	Brooke, Virginia, USA: creek 200 m west of junction of highways 608 and 629: N33.38687° W77.380700°	Patapsco Formation	Early Cretaceous	Doyle & Hickey (1976), Powars & Bruce (1999)
L3003	Golden Grove, South Australia: northwest margin of large quarry on One Tree Road: S34.7811° E138.73932°	Golden Grove beds	Eocene	McCallum (1990)

Table 2. New localities for fossil logs in quartz sandstone.

similar age and rib count (Runnegar 1992). Not only do they fall on different growth arrays (Fig. 3A), but the larger supposedly 'inflated' specimen has a wider supposed 'contraction rim' than the smaller and supposedly 'contracted' specimen. If the smaller one contracted from a specimen as large as and with ribs as wide as the larger one, its rim should be larger. Furthermore, the midrib, interpreted as a gut of an annelid or other soft bodied creature (Jenkins 1996), is wider in the narrow ribbed and supposedly contracted specimen, than in the wider ribbed and inflated specimen. Midrib width is a consistent feature differentiating *Dickinsonia costata* from *D. tenuis*, so unrelated to satiation, decay or orientation.

Histograms of width and length in *D. costata* are both strongly negatively skewed (Fig. 4B). Because these are populations in place of growth, both observations indicate isometric indeterminate growth, typical of fungi, plants and colonial animals (Retallack 1994, Peterson *et al.* 2003). The largest *Dickinsonia* at 1400 mm long (Jenkins 1996) is 28 times the modal length of 50 mm (Fig. 4B), a highly significantly skewed distribution. *Dickinsonia* continued to grow until covered by sediment, like seaweeds, trees, lichens, bryozoans and other colonial organisms with indeterminate growth. In contrast, free living worms such as *Spinther arcticus* and *Nereis diversicolor* show allometric determinate growth, very distinct from *Dickinsonia* (Runnegar 1982). Polyps and jellyfish also show determinate growth to asexual or sexual reproductive size (Gand *et al.* 1996). Like most metazoans,

Locality	Specimen	Taxon	Burial depth (km)	Log width (mm)	Log thickness (mm)
L3003	F36246	Dicot?	0.066	9.53	2.03
L3002	F36247	Dicot?	0.5	18.66	3.12
L3002	F36247	Dicot?	0.5	5.96	1.18
L3002	F36247	Dicot?	0.5	7.52	1.01
L3002	F36247	Dicot?	0.5	4.11	1.75
L3002	F36247	Dicot?	0.5	12.77	1.56
L2998	F36241A	Glossopterid?	1.27	22.32	1.52
L2998	F36241B	Glossopterid?	1.27	16.4	1.92
L2998	F36241C	Glossopterid?	1.27	23.33	1.69
L3000	F36243A	Conifer?	1.5	23.41	2.23
L3000	F36243B	Conifer?	1.5	11.21	1.16
L3000	F36243C	Conifer?	1.5	13.64	1.34
L3000	F36243D	Conifer?	1.5	17.48	1.57
L3001	F36244A	Dicot?	1.759	24.22	2.53
L3001	F36244B	Dicot?	1.759	29.62	2.2
L3001	F36244C	Dicot?	1.759	6.69	1.18
L3001	F36244D	Dicot?	1.759	11.01	1.55
L3001	F36244E	Dicot?	1.759	28.27	1.69
L3001	F36244F	Dicot?	1.759	12.99	1.06
L3001	F36244G	Dicot?	1.759	22.06	3.18
L3001	F36244H	Dicot?	1.759	14.42	1.84

Table 3. New data on compaction of fossil logs in quartz sandstone.

their growth slows and then ceases soon after sexual maturity near a modal size (Peterson *et al.* 2003).

Decay of thickness indicated by depth measurements

Dickinsonia is a 'resistant' Ediacaran fossil like *Tribrachidium* and *Parvancorina* (Wade 1968) preserved as a raised impression (on the underlying bed), unlike other associated Ediacaran fossils (Retallack 1994, Gehling 1999). Most specimens are concave on the soles of overlying beds. Because the best specimens are enhanced by weathering of loose slabs, parts and counterparts are rarely collected (Gehling 1999): for example, a single specimen of *Dickinsonia costata* (SAM P41166a,b) and one of *D. rex* (SAM P40200). In both cases, the upper side is a concave ribbed mark on the sole of the overlying bed, and the under side is a convex mark on the top of the underlying bed (Wade 1968, Retallack 1994). My measurements demonstrate that *Dickinsonia* fossils range from 0 to as much as 3 mm thick between part and counterpart (Fig. 3). This gap contains loosely cemented grains at its base and in a few cases some hematitic clay (Gehling 1999). The upper concave impression is smoothly finished with a fine patina of hematite, distinct from its convex counterpart, which is more friable, with fainter and less distinct ribbing and midline (Gehling 1999). Thus, *Dickinsonia* ribbing was unifacial, and a portion of the impression was supported by sand from below. This was subtracted from the total depth of impressions in estimating thickness and its subsequent compaction due to burial.

Thickness measurements of *Dickinsonia* do not show clear growth arrays, but instead

Burial depth (km)	Reference to burial depth	Mean height/width of tube cells	Standard deviation of mean	Number of cells measured	Taxon
1.45	Bertrand-Sarfati *et al.* (1991)	0.45	0.07	11	*Spongiophyton nanum*: Chaloner *et al.* (1974 pl. 124, fig. 1)
1.45	Bertrand-Sarfati *et al.* (1991)	0.48	0.10	4	*Spongiophyton nanum*: Chaloner *et al.* (1974 pl. 121, fig. 7)
3.784	Poole *et al.* (1976)	0.48	0.09	30	*Spongiophyton minutissimum*: Gensel *et al.* (1991 text-fig. 5D)
12.192	Beaumont *et al.* (1988)	0.48	0.05	4	*Prototaxites* sp: Strother (1988 fig. 8-2)
12.192	Beaumont *et al.* (1988)	0.44	0.14	5	*Prototaxites* sp: Strother (1988 fig. 8-4)
18.4	Kent (1980)	0.47	0.11	29	*Thucomyces lichenoides*: Hallbauer *et al.* (1977, pl. III, fig. 24)

Table 4. Measurements of compacted microstructure of fossil fungi and lichens.

great variability for fossils of comparable width (Fig. 3B). All the specimens measured were distinct, but vary from thick specimens with marked ribbing to thin specimens with weak ribs. The size distribution of preserved thickness is bimodal, unlike the thickness for each width predicted from a growth equation of Fig. 3, which shows a left-skewed, unimodal curve like that of thickness and length (Fig. 4A). Bimodal or polymodal distributions would be expected from the contribution of bedding planes of different biomat age with fossils in different stages of decay. A unimodal skewed curve supports the idea of indeterminate growth in thickness, though more constrained in rate than growth in width and length.

This pattern of thickness variation is comparable with that of fossil leaves (Ferguson 1985) and fungi or lichens (such as *Nematothallus* of Strother 1988, Hueber 2001), which show variable decay and thickness loss before burial. The first tissues to

decay in leaves are parenchymatous palisade and mesophyll cells, then the cuticle itself thins and is breached, leaving a 'leaf skeleton' of tracheids as the last outline (Ferguson 1985). Phycobiont and hymenial tissues of lichens and fungi wilt and decay before mycobiont hyphae (Brodo *et al.* 2001). From this perspective, the variability in thickness of *Dickinsonia* is evidence for decay before burial. Thickness of undecayed but burial-compacted specimens is represented by the thickest specimens, and the growth equations shown in Fig. 3.

This pattern of decay and thinning with modest deformation, is distinct from that of living (Norris 1989, Bruton 1991) and fossil jellyfish (Gand *et al.* 1996, Hagadorn *et al.* 2002) or worms (Conway Morris *et al.* 1982), which form clotted irregular masses, torn and exploded fragments, and wrinkled skeins. The observed decay and thinning of *Dickinsonia* is also distinct from osmotic shrinkage, wilting and desiccation, which
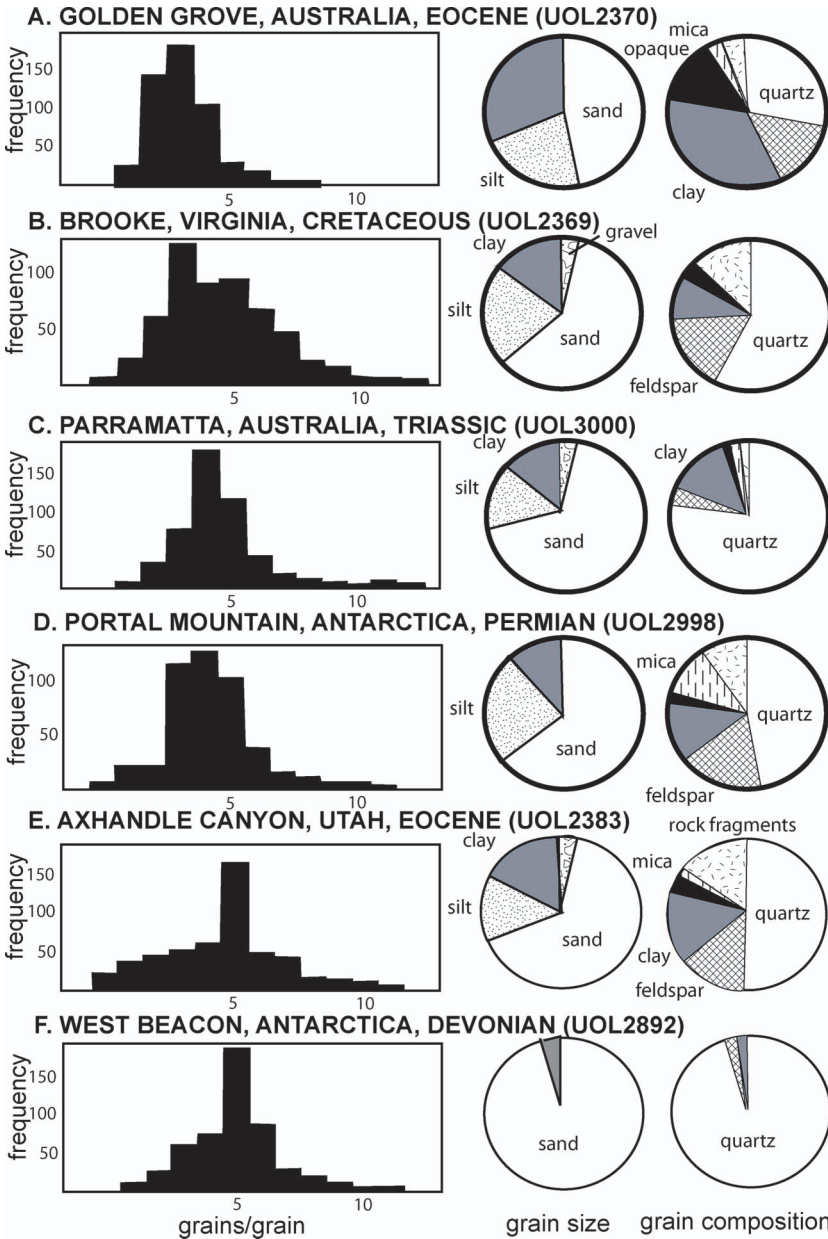
Fig. 2. Petrographic data on matrices of fossil logs used to construct compaction curve of logs for comparison with burial compaction of *Dickinsonia* (Fig. 6), showing grain contacts per grain as an indication of burial compaction (histograms), and grainsize and composition as indications of mechanical strength (pie diagrams). All data are from point counting petrographic thin-sections.

form prominent wrinkles, folds, and twisting in pickled and dried natural history specimens of marine invertebrates. Thick gelatinous bodies, untethered to the substrate, deform irregularly upon death or distress.
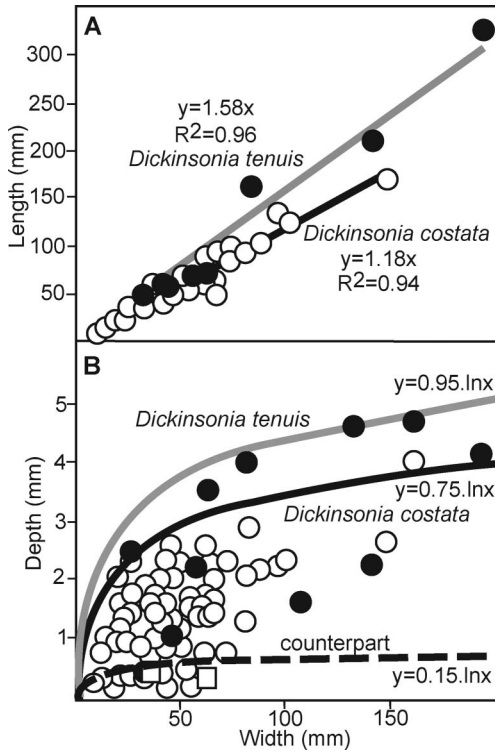
Fig. 3. Variation in width vs length and thickness of specimens of *Dickinsonia costata* (open circles) and *D. tenuis* (closed circles) from the Ediacara Hills and Flinders Ranges, South Australia. Open squares are specimens of counterparts, showing the portion of the raised impression filled with sand from below. Growth in width and length was indeterminate and isometric, but growth in thickness is obscured by effects of decay.
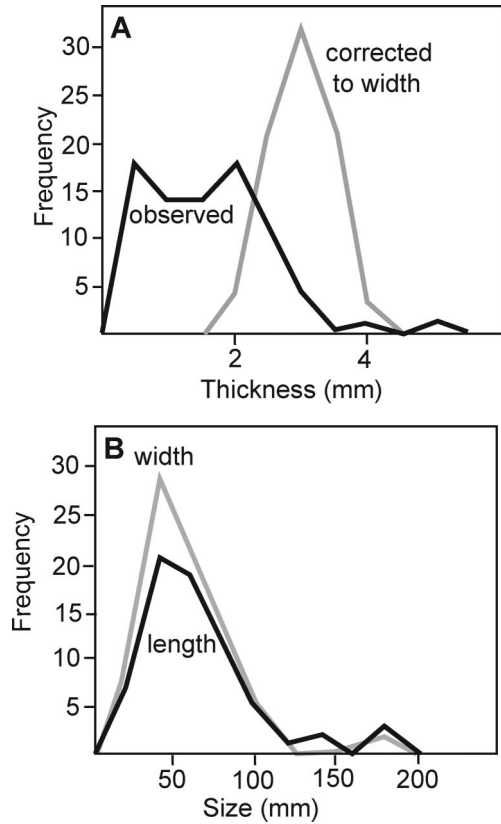

Fig. 4. Histograms of width, length, and thickness of *Dickinsonia costata*. Also shown are preburial thicknesses corrected for decay using the inferred growth curves of Fig. 3. All curves show the strong left skew of indeterminate growth.

Burial compaction resistance indicated by depth measurements

Some specimens of *Dickinsonia*, presumably undecayed, make a remarkably strong impression in quartz sandstones that have been buried 1.5 – 5.8 km, much like fossil logs and leaves (Retallack 1994). My previous observations are further quantified here by application of subsequent compaction algorithms (Sheldon & Retallack 2001), and also by comparison with burial compaction of subsequently recognized fossil fungi and

lichens. Compaction of fossil fungi and lichens can be inferred from deformation of hyphae known to be tubular in permineralized specimens and modern analogs (Hallbauer *et al.* 1977, Hueber 2001), but flattened to ellipses in compression specimens (Chaloner *et al.* 1974, Strother 1988, Gensel *et al.* 1991). The compaction of lichen microstructure with depth (Fig. 5) follows the same compaction curve as low-density soils, Andisols and Spodosols (Sheldon & Retallack 2001). Compaction of fossil logs is estimated assuming that they were cylindrical objects, and maintained their width but not thickness with burial
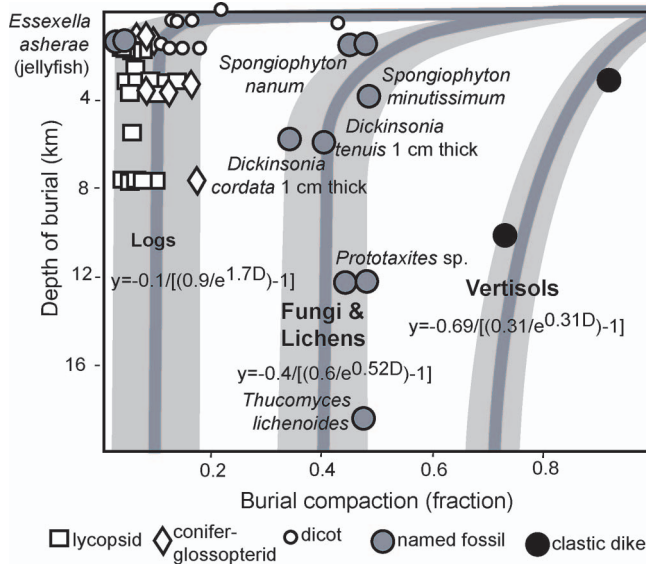
Fig. 5. Fractional compaction predicted from standard equations of Sheldon and Retallack (2001) compared with observed compaction with depth of palaeosols, lichens, logs, jellyfish and *Dickinsonia*. Compaction was measured from ptygmatic folding of clastic dykes in Vertisol palaeosols, from microstructural deformation of fossil fungi and lichens (*Thucomyces, Spongiophyton, Prototaxites*), from compressed thickness of fossil logs, and from current thickness compared with assumed original thickness of 1 cm for the Ediacaran fossil *Dickinsonia*, which was as compaction-resistant as fossil fungi and lichens.

compression (Rex & Chaloner 1983). Fractional compaction of fossil logs follows the same curve with increasing depth of burial (Fig. 5) as woody peats and coals (Histosols of Sheldon & Retallack 2001).

Estimating compaction of *Dickinsonia* is more difficult, because it was neither ellipsoidal nor spherical in shape. Two observations suggest that they were low ground-hugging organisms: (1) wrinkled specimens partially folded over themselves (Fig. 1D) and (2) undeformed ripple-marked foresets of covering sediment (Fig. 1C). Many specimens have been found slightly folded over themselves (Gehling *et al.* 2005), and the one figured here (Fig. 1D) shows the maximum extent of overlap, only 4 mm at the margin, which suggests firm attachment of most of the body to the substrate. Currents inferred from overlying ripple marks should have entrained them if they were free living (Schopf & Baumiller 1998). No *Dickinsonia* are known upside down or folded in half.

A marked zone of sediment disruption is visible in partly dismembered specimens (Gehling *et al.* 2005). They were either cemented to the substrate like oysters or corals (Valentine 1992), rooted by rhizines like crustose lichens, or attached to subsurface rhizomorphs like some fungi (Retallack 1994). *Dickinsonia* fossils have been found on slabs as thin as 8 mm, with no evidence that they protruded through the top, or that sediment swirled around them during burial. An 8-mm-thick bed would have been 1.4 cm thick before compaction by 5.8 km of overburden (following algorithm for quartz sand and Spodosols of Sheldon & Retallack 2001), so *Dickinsonia* are unlikely to have been thicker than 1 cm. A comparison of that thickness to present thicknesses (Fig. 4) shows that *Dickinsonia* was at least as compaction resistant as fossil fungi and lichens (*Prototaxites, Spongiophyton*, *Thucomyces*) and much more compaction-resistant than fossil logs (Fig. 5). The 1-cm case is an upper

limit: *Dickinsonia* would have been even more compaction resistant if thinner in life. Presumably *Dickinsonia* had a strong bio-polymer, such as the chitin of fungal cell walls (Retallack 1994).

Newly applied compaction algorithms (Sheldon & Retallack 2001) also show that *Dickinsonia* was not as compaction-resistant as most soils, such as Vertisols used to calibrate the compaction equation by un-ravelling their ptygmatically folded clastic dykes (Fig. 5). *Dickinsonia* was much less compacted than jellyfish *Essexella asherae* (Fig. 5) preserved in siderite nodules, which themselves were compaction-resistant (Retallack 1994). Cambrian jellyfish from Wisconsin (Hagadorn *et al.* 2002) and Sweden (Cherns 1994) have significant (though unmeasured) relief, but their local radial synaeresis cracking and ferruginiza-tion suggest that some of these fossils gained strength from mineralization by siderite. Such sideritic nodules or ferruginized haloes have not been found around *Dickinsonia*. In other cases, relief of Cambrian jellyfish fossils came from natural casts of sediment ingested during death throws (Hagadorn *et al.* 2002). Such internal moulds are known in Ediacaran fossils (*Protoechiuris* and *Ernietta* of Glaessner, 1984, p. 82), but not with *Dickinsonia*. Supposed medusae from Ordovician sandstones of Morocco also have a relief and size similar to Ediacaran fossils (Samuelson *et al.* 2001), but their U-shaped gut indicates that they were not jellyfish but eldoniid echinoderms, and their finely pebbled texture suggests a spicular skeleton (Geyer 1994, Zhu *et al.* 2002).

Other indications of affinities and taphonomy of *Dickinsonia*

My measurements of *Dickinsonia* indicate modes of growth and decay and burial compaction more like those of lichens, plants, algae, xenophyophores, or colonial organisms than of worms, polyps or jelly-fish. From this perspective, the following paragraphs reevaluate a variety of published arguments concerning the affinities and taphonomy of *Dickinsonia*.

Retraction rim, tentacles, pseudopodia or growth increment?

Marginal halos around *Dickinsonia* have been interpreted as impressions of fully hydrated animals that were desiccated to a smaller size, and a specimen with thinner segments regarded as shrunken from a creature like one with wider segments and the same segment count on the same slab (Fig. 1A; Wade 1972, Runnegar 1982), as would be expected of a gelatinous soft-bodied creature. These two specimens fall on different growth arrays (Fig. 3A) and are regarded here as different species, not pre-servational variants. The marginal haloes are not only fainter and thinner than the main impressions, but have finer lineation on both large and small specimens (Fig. 6B). Marginal haloes are clear in well-preserved specimens on elephant-skin-tex-tured surfaces regarded as microbial mats (Figs 1A, 6), as well as extensively decayed specimens on less obviously microbial sur-faces (Fig. 1E). These observations falsify the retraction hypothesis, because retracting ribs should leave grooves of the same scale, and marks in sediment or microbial mats would not persist with advanced decay and dispersion of allelopathic chemicals at the surface.

The filamentous marginal haloes have also been interpreted as tentacles of jellyfish (Sprigg 1947, Harrington & Moore 1956), or as a soft flexuous foot extending from be-neath a chitinous dorsal carapace (Fedonkin 2002). In the xenophyophore interpreta-tion championed by Seilacher *et al.* (2005) they could be pseudopodia. The principal objection to all three views comes from specimens that show a clearly preserved
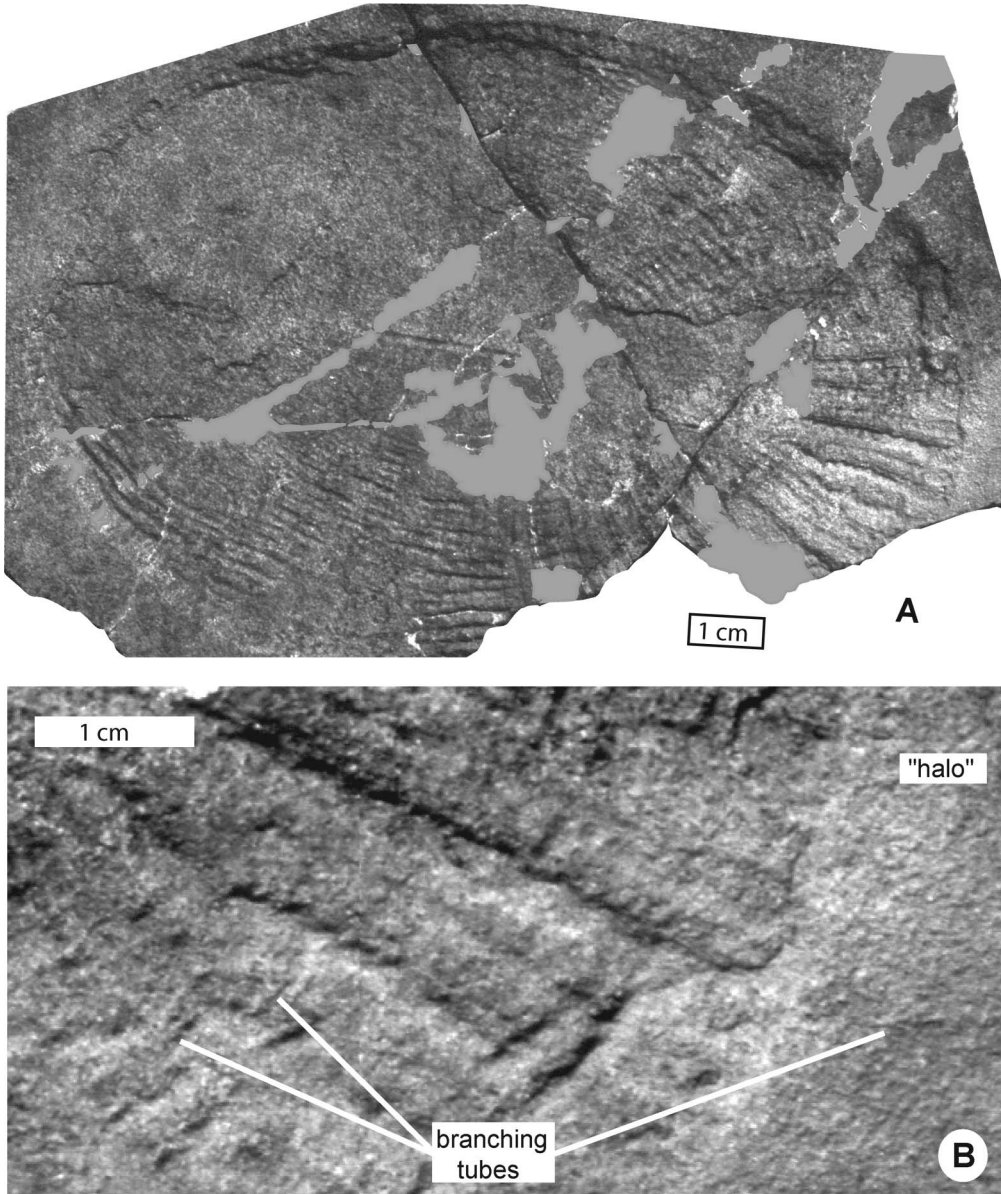
Fig. 6. An exceptionally large specimen of *Dickinsonia costata* (**A**) from the late Precambrian Ediacara member of the Rawnsley Quartzite in Brachina Gorge, South Australia, showing extensive microtubular construction in enlarged portion (**B**). Condon Museum, University of Oregon (F34285).

filamentous margin, yet extensively decayed central portion (Fig. 1E). Protist, jellyfish, arthropod and molluscan carapaces are commonly preserved without more delicate appendages, tentacles or feet, but the preservation of feet without carapaces is unknown.

Yet another interpretation of the halo is a rhizinous foundation for a future growth increment of a lichen (Retallack 1994). This

interpretation is especially suggested by a specimen showing a reaction rim to an adjacent specimen short of actual contact (Fig. 1B), and other specimens showing tubular features in the marginal halo like those of the main part of the fossil (Fig. 6B). Such a rim would not only have been an allelopathic advanced defense, but enabled repair of heavily damaged specimens, which is an alternative explanation to double shrinkage proposed for a specimen illustrated by Gehling *et al.* (2005, fig. 8). Persistence and regeneration from margins of lichens is common after death and decay of their centres (Brodo *et al.* 2001).

Fractal-tubular construction

The sandstone matrix of South Australian *Dickinsonia* precludes histological study, but large specimens show abundant branching tubular structures of several different size grades all coarser than sand grains and finer than conspicuous ribbing (Fig. 6). These are unlikely to be individual hyphae of fungi or actinobacteria, because they are much too large (0.5–1 mm diameter). The tubular structures create a felt-like fabric orthogonal to the broad ribs, but in the marginal halo, tubes branch and splay radially away from the fossil, like lichen rhizines or fungal rhizomorphs. The specimen best showing these features (Fig. 6) is large (16 cm wide), deeply impressed (4 mm: see Fig. 3B) and presumably little decayed.

These tubular features of large *Dickinsonia* are like those found by Narbonne (2004) in rangeomorph Ediacaran fossils from Newfoundland preserved in shale. Comparable construction of laterally linked branching tubes is seen in impressions of 'spindle' Ediacarans at Mistaken Point, Newfoundland (Clapham & Narbonne 2002, Peterson *et al.* 2003), in permineralized petalonaman Ediacarans of Namibia (Pflug 1973), and is compatible with the 'pneu' architecture

proposed by Seilacher (1989). New discoveries by Narbonne (2004) thus confirm that permineralized Ediacarans of Namibia preserve original histology, rather than later fungal or other replacement (Retallack 1994). Namibian permineralizations also show that the hollow tubes (0.1–2 mm diameter) are constructed of densely woven, tubular cells (1–5 μm) and interspersed, dark spherical cells (4–5 μm: Pflug 1973, 1994). This histology is unlike that of any animal or plant, and most like podetia (megascopic tubes), mycobionts (tubular cells) and phycobionts (dark spherical cells) of lichens (Retallack 1994).

Tubular branching structures 1–2 mm in diameter have been illustrated in a decayed *Dickinsonia* by Jenkins (1996, fig. 4.2D), who interpreted them as intestinal caecae. This would be unlikely anyway by the biological model of an annelid or polychaete worm, because they run across the segments. The tubes could be unravelled portions of a fractal tubular construction as outlined by Narbonne (2004). Very large tubular intestinal caecae are inferred for *Dickinsonia* from Russia (Dzik & Ivantsov 2002), but these lack well-defined margins and look more like exaggerated growth rugae, as found in lichens, fungi, jellyfish or polyps. Such ridges are interpreted as evidence of muscular contraction by Gehling *et al.* (2005). These features run across almost all segments, so also are incompatible with interpretation as annelid internal organs. Indistinct oval welts also without well-defined margins have been interpreted by Dzik & Ivantsov (2002) as gonads. They could equally be localized areas of arrested growth or decay. The central axis of *Dickinsonia* and plausibly allied genera has been interpreted as a gut (Jenkins 1996, Ivantsov 2004), but in most cases it is a simple crease, and no clear mark of a mouth or anus is visible. By Pflug's (1973, 1994) and Narbonne's (2004) fractal-tubular construction model, this could have been the central axis from which others

branched. Ubiquitous fine-tubular structures of *Dickinsonia* (Fig. 6B) are unlike the histology of animals, and more like fungi and lichens.

Trails, rhizomorphs or decayed fairy rings?
Dickinsonia has been interpreted as a worm or other motile invertebrate on the basis of supposed trails and resting impressions on the same slabs. The best of these is a large slab (Fig. 7A) with numerous '*Aulozoon*' (informal name of Seilacher *et al.* 2003) and *Phyllozoon hanseni* Jenkins & Gehling 1978 on 'elephant-skin-textured' surfaces (microbial mat), together with four *Dickinsonia costata* and a single *Pseudorhizostomites howchini* Sprigg, 1949, the last of which is probably a gas escape structure (Seilacher *et al.* 2005). *Phyllozoon* and *Dickinsonia* are preserved as concave imprints on the sole of the bed (hypichnia of Martinsson 1970). Some '*Aulozoon*' are full-relief sandstone moulds (exichnia) 1–2 mm thick and 2 cm wide, others are more deeply embedded (hypichnia of Martinsson 1970). Crisply defined '*Aulozoon*' run both above and below clear impressions of *Phyllozoon*. The three *Dickinsonia* protruding from behind '*Aulozoon*' were all deeper in the slab, so originally above '*Aulozoon*' and the surficial biomat. These topological details are generally agreed (Runnegar 1992, Seilacher *et al.* 2003, 2005), but interpretation of this slab is a challenge.

'*Aulozoon*' may have been a trail, as interpreted by Glaessner (1969). A worm burrow is implied by Jenkins's (1995) identification of these fossils with the more inflated *Palaeophycus tubularis* Hall, 1847). The flattened elliptical cross-section of '*Aulozoon*' was considered evidence of a flatworm burrower by Seilacher *et al.* (2003, 2005). By any of these interpretations, neither *Dickinsonia* nor *Phyllozoon* on this slab could have made '*Aulozoon*' because they are too large and not on the same plane

as the trail or burrow. Other problems are physical difficulties for flatworms pushing through biomatted sand, the extreme flattening required if this were a burrow with more nearly circular cross-section of a coelomate worm, and the crisp preservation if these were trails remaining from before overgrowth of the microbial mat (Seilacher *et al.* 2005). I agree with Gehling *et al.* (2005) that '*Aulozoon*' was a body fossil, and also follow the interpretation of Seilacher *et al.* (2005) that it lived within the biomat and sediment like *Phyllozoon*, rather than being tangled with other winnowed fossils (Gehling *et al.* 2005). Although conventionally interpreted as a sea pen, some *Phyllozoon* on the slab are intergrown (Fig. 7A; see also illustrations of Runnegar 1992, Droser *et al.* 2005) like interpenetrated *Pteridinium* thought to have lived within sediment (Grazhdankin & Seilacher 2002). If *Phyllozoon* lived within the sediment, then so did '*Aulozoon*', because they are intertwined and equally fresh impressions. An alternative interpretation is that '*Aulozoon*' was a mycelial rhizomorph like those of modern bootlace fungi (*Armillaria mellea*: Basidiomycetes; Mihail & Bruhn 2005) or a system of lichen rhizines like those of modern crustose ascolichens (*Xanthoparmelia*; Paradise 1997). By these interpretations, *Dickinsonia* may have been the mushroom or thallus of '*Aulozoon*'. This is suggested by location of all four *Dickinsonia* at the end of rounded terminations of '*Aulozoon*'. If this is a coincidence, it is a rare one (about 1 in 16 chances for even odds of on vs off alignment). In any case this spectacular specimen (Fig. 7A) does not show trails or burrows of *Dickinsonia*.

Other fossils interpreted as trails, resting marks, or tool marks of *Dickinsonia* (Ivantsov & Fedonkin 2001, Fedonkin 2002) appear to be variably decayed specimens. Some of these faint markings are raised impressions (negatives on capping sandstone, number 2 of Fig. 1E) and would
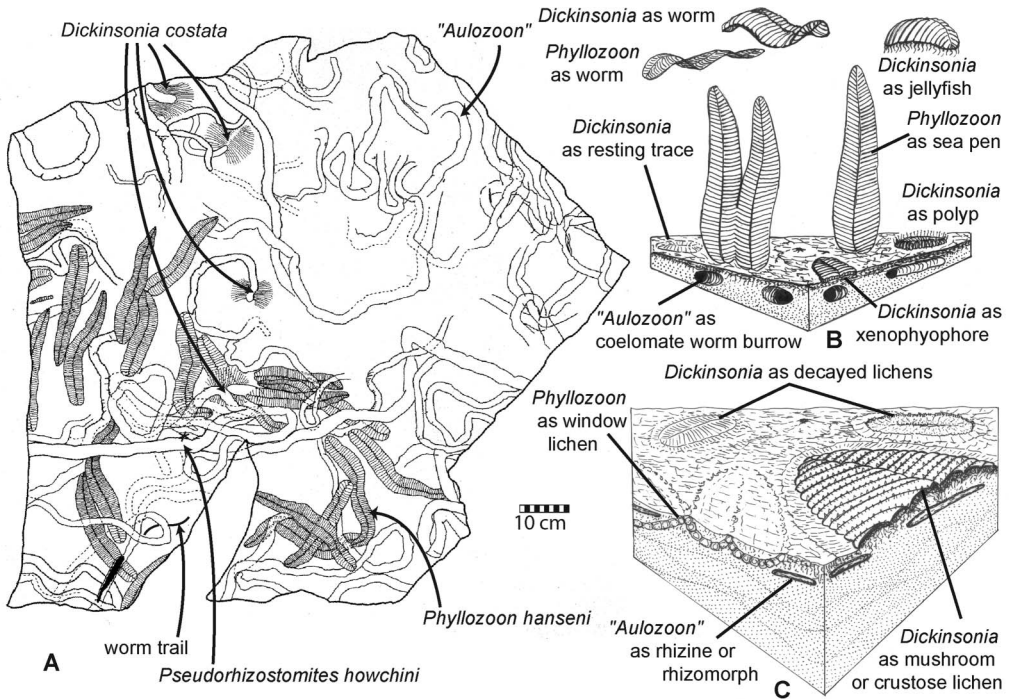
Fig. 7. **A**, portion of large slab from the Ediacara Member of the Rawnsley Quartzite in Bathtub Gorge, Flinders Ranges, now on display at the South Australian Museum, showing 23 *Phyllozoon hanseni*, numerous '*Aulozoon*' sp., four *Dickinsonia costata*, at least one narrow worm trail, and widespread microbial mat with elephant-skin texture (after Seilacher *et al*. 2003, 2005, Gehling *et al*. 2005). Also shown are alternative animal (**B**) and lichen-fungal (**C**) interpretations.

call for an unusual level of mucus production for such large flat creatures, to suppress microbial growth on elephant-skin-textured surfaces, and bind sediment into a platform. Others of these faint markings are sunken impressions (positives on capping sandstone, numbers 3 and 4 of Fig. 1E), but these are the most effaced, and lack internal rib impressions, yet curiously preserve the filamentous marginal halo found also around well-preserved specimens. These are not successive displacements and reattachments or grazing traces of a single individual because they are slightly different in size (Fig. 1E). None of the supposed trails shows lateral undulation, bulldozed rims, brush marks, or backfills, that would indicate motion of a creeping or swimming

organism. All these supposed trails and resting marks show ghost oval outlines, not a continuous swath of a moving individual. Lack of such indications of motion was also noted by Gehling *et al*. (2005), who argued for a worm-like *Dickinsonia* moving intermittently and feeding by means of a digestive foot, rather than a mouth. Such diffuse feeding mechanisms are characteristic of fungi, lichens and xenophyophores.

These supposed trails are interpreted here as decayed specimens, at the lower extreme of distinctness and measured thickness (Fig. 3B). The preservation of marginal rhizines with central necrosis of the colony is common in lichens, which grow outward from a center. Arrangement of these specimens in arcs suggestive of a trail can also be

explained by the common alignment of fungi, generally known as fairy rings. These vary from simple circles to more complex swaths of mushrooms. The circular arrangement is due to peripheral fruiting of a central buried mycelial mass (Ingold 2000). A prediction of the fairy ring model is that complete circles will be discovered on suitably large exposures of single bedding planes, as suggested by many almost complete rings (for example, Fig. 3C).

Mineralization or biopolymer?

Some *Dickinsonia* are wrinkled and deformed, marginally overfolded, and slightly torn, but this is not always a distortion of ideal symmetry. The left-hand side of one specimen (Fig. 1D) has grown wider than the right-hand side (Fig. 1D). In other cases, lobation of margins (Fig. 1A) gives a spindle-like outline rather than subrectangular to ellipsoidal shape (also in Fig. 1A). Such localized distortion is untransferred to other parts of the same specimen as wrinkles or splits, which falsifies the view that these were coherent, bilaterally symmetrical, chitinous, dorsal carapaces (Fedonkin 2002). Other specimens with bumps and ridges have been thought to be thin bodies draped over an irregular microbial substrate (Gehling *et al.* 2005), but bumps and ridges could also have been propagated by overgrowth of a lichen or xenophyophore. In none of the distorted and irregular specimens (see also Wade 1972, Runnegar 1982, Jenkins 1992) is there a hint of angular shards or brittle fracture, so well known from burial compaction of trilobite cephala (Webster & Hughes 1999).

These observations falsify the idea of agglutinate or other mineral skeletons or rigid death masks of pyrite, siderite or calcite formed early during burial (Wade 1968, Gehling 1999, Gehling *et al.* 2005). No pyrite, siderite or calcite has been found with South Australian specimens. Many

South Australian Ediacaran fossils are ferruginized in the modern outcrop, but that iron shows smooth, felty and tubular patina (Fig. 6), not knobby, framboidal or cubic textures after pyrite. South Australian Ediacaran fossils are not yellow or smelly with jarosite, a common weathering product of pyrite (Retallack & Dilcher 1981). Pyrite associated with Russian Ediacaran fossils occurs as either isolated framboids (Steiner & Reitner 2001) or nodules, which obliterate the ribbing of *Dickinsonia*, enveloping it in thick ellipsoidal pyrite nodules with a coarsely knobby surface (Dzik & Ivantsov 2002). Thus, pyritization obscures rather than conserves the characteristic ribbing of Russian *Dickinsonia*. If pyritic death masks were the explanation, then specimens most effaced by pyritization should have the most relief, contrary to observation (Fig. 1E). Heavily pyritized Russian *Dickinsonia* should be examined microscopically in polished thick section, a technique that has been invaluable in studying the histology of fossil plants (Matten 1973). Silica-permineralized Ediaracan fossils from Namibia have isolated carbonate crystals (Pflug 1973), which may have been a lichen pruina (Retallack 1994), but show no evidence of pervasive biologically induced mineralization. An unrealistically steep redoxocline would be needed to precipitate pyrite beneath only 1–2 cm of sediment as envisaged by Gehling (1999), even in Neoproterozoic atmospheric oxidation levels indicated by palaeosols (Retallack 2001). Finally, the explanation of pyritic death mask preservation is only invoked for a few Neoproterozoic fossils, including *Dickinsonia*, and has not been demonstrated for other Ediacaran fossils or for soft-bodied fossils at any other time in Earth history.

The fine hematitic patina of many Ediacaran fossils is comparable with microbial encrustation and precipitation of iron hydroxides before burial, as demonstrated

by Spicer (1977) for angiosperm leaf fossils in ferruginized sandstones deposited in fluvial levees of the Cretaceous Dakota Formation in Kansas (Retallack & Dilcher 1981). These leaf impressions have relief proportional to their cuticle thickness and strength of venation. Woody fruits were compacted by burial much less than associated ferruginous leaves (Crane & Dilcher 1984). Ferruginization with a few microns of fine iron oxides before burial greatly improved impressions of fine venation in this sandy inorganic matrix, but that thin death mask played a subordinate structural role to lignification in creating relief and resisting burial compaction.

Global change implications

Dickinsonia has been used to place constraints on atmospheric oxygenation, assuming oxygen requirements and diffusional limitations of an animal without a circulatory system (Runnegar 1982). If on the other hand *Dickinsonia* was a lichen (Retallack 1994), it would have produced oxygen. Deepened, prolonged and accelerated soil formation under lichens would have promoted carbon sequestration, and aided in global cooling more effectively than pre-existing microbial mats (Retallack 2004). It may not have been a coincidence that the appearance and evolutionary diversification of Ediacaran fossils from small, less organized fossils to large, regularly symmetrical *Dickinsonia* (Fedonkin 1992, Jenkins 1992, Williams & Schmidt 2003) was during sequential episodes of global glaciation (Hoffman *et al.* 1998), which have been dubbed Snowball Earth (Kirschvink 1992). Large three-dimensional sessile lichens or fungi in shallow marine and intertidal environments would have provided food, shelter and environmental partitions for coelomate infaunal invertebrates, thought to have been coeval with Ediacaran fossils from associated small

burrows (Seilacher *et al.* 2003, 2005) and fossil embryos in phosphorites (Xiao *et al.* 2000).

Conclusions

Falsifying features for various biological interpretations of *Dickinsonia* are shown in bold in Table 5. The popular worm interpretation (Termier & Termier 1968, Wade 1972, Conway Morris 1979) for *Dickinsonia* is falsified by fractal-tubular construction (Fig. 6), isometric indeterminate growth (Figs 3–4), allelopathic reaction to other individuals (Fig. 1B), and strong resistance to burial compaction (Fig. 5). Interpretations of *Dickinsonia* as jellyfish (Harrington & Moore 1956) or polyps (Valentine 1992) founder not only on the obvious bilateral symmetry, quilt-like structure and lack of marginal musculature (Seilacher 1989), but on stronger resistance to burial and compaction than genuine fossil jellyfish (Fig. 5). A xenophyophoran interpretation (Zhuravlev 1993, Seilacher *et al.* 2005) is unlikely because 1.4-m-long *Dickinsonia* was much larger than the largest living xenophyophoran (25 cm: Tendal 1972), though not too large compared with other siphoneous unicells, such as those of the chlorophyte seaweed *Cladophora* (Runnegar 1995). Key falsifying features of *Dickinsonia* for a xenophyophore interpretation include bilateral symmetry (Fig. 1A), highly variable microtube diameter (Fig. 6), and evidence for plastic deformation rather than brittle failure or fragmentation of an agglutinative-mineral skeleton (Fig. 1D). Only the fungal-lichen model remains unfalsified (Table 5), however unappealing it may seem compared with lively, leaping, swimming *Dickinsonia* (Fig. 7B–C). Suggestions that Ediacarans are a completely extinct clade (Seilacher 1992, Fedonkin 2003) also remain unfalsified, but only generate testable predictions by virtue of their phyletic relationship with other groups discussed.

Lichen	Non-lichenized fungus	Xenophyopore protist	Cnidarian Polyp	Cnidarian jellyfish	Polychaete worm	Annelid worm	Turbellarian worm
100% below	100% below	81% below	81% below	75% below	69% below	69% below	63% below
Areoles	Lamellae	Tubes	Wrinkles	Wrinkles	Segments	Segments	Wrinkles
Areolae around midline	Lamellae around midline	Tubular alternate growth	Mesenteries pseudo-bilateral	Mesenteries pseudo-bilateral	Segments distorted by muscles	Segments distorted by muscles	Wrinkles torqued at midline
Central stipe	Central stipe	Growth initial	Mesenteries pseudo-bilateral	Mesenteries pseudo-bilateral	Gut	Gut	Gut
Isidial initial	Hymenial stipe	Cell initial	Mesenteric initial	Mesenteric initial	Pharyngeal pouch	Pharyngeal pouch	Pharyngeal pouch
Rhizines	Rhizines	Pseudopodia	Tentacles	Tentacles	Parapodia	Parapodia	Parapodia
Apothecia	Peridioles	Resting cysts	Elliptical gonads	Elliptical gonads	Elliptical gonads	Elliptical gonads	Elliptical gonads
Fairy ring	Fairy ring	Trail	Trail	Trail	Trail	Trail	Trail
Decayed thallus	Decayed thallus	Degraded test	Resting trace	Resting trace	Resting trace	Resting trace	Resting trace
Growth rugae	Growth rugae	Growth rugae	Growth rugae	Growth rugae	Large intestinal caecae	Large intestinal caecae	Large intestinal caecae
Podetia	Scyphi	**Subordinate tubes unexplained**	Nephridia	Nephridia	Small intestinal caecae	Small intestinal caecae	Small intestinal caecae
Up to 1.4 m long	Up to 1.4 m long	**1.4 m unlikely for unicell**	Up to 1.4 m long	Up to 1.4 m long	Up to 1.4 m long	Up to 1.4 m long	**1.4 m unlikely**
Isometric indeterminate growth	Isometric indeterminate growth	Isometric indeterminate growth	Isometric indeterminate growth	Isometric indeterminate growth	**Isometric growth unexplained**	**Isometric growth unexplained**	**Isometric growth unexplained**
Areoles upper side only	Lamellae upper side only	Xenophyae upper side only	Tentacles upper side only	Umbrella pellicle upper side	**Unifacial structure unexplained**	**Unifacial structure unexplained**	**Unifacial structure unexplained**
Competitive reaction rim	Competitive reaction rim	Competitive reaction rim	Competitive reaction rim	**Thickening unexplained**	**Thickening unexplained**	**Thickening unexplained**	**Thickening unexplained**
Raised impression of crustose habit	Raised impression of crustose habit	Agglutinate mineralized exoskeleton	**Raised impression unexplained**	**Raised impression unexplained**	**Raised impression unexplained**	**Raised impression unexplained**	**Raised impression unexplained**
Compaction resistance due to chitin	Compaction resistance due to chitin	Agglutinate Mineralized exoskeleton	**Compaction resistance unexplained**	**Compaction resistance unexplained**	**Compaction resistance unexplained**	**Compaction resistance unexplained**	**Compaction resistance unexplained**

Table 5. Biological models for features of *Dickinsonia* (with falsifying features shown in bold).

Dickinsonia is a pleasingly symmetrical and complex fossil evocative of biological complexity (Jenkins 1996), but even organisms as simple as fungi and lichens create mushrooms and morels of startling elegance (Retallack 1994). Tidal flat to shallow subtidal habitats (Jenkins *et al.* 1983) and community tiering (Clapham & Narbonne 2002) do not shed light on affinities because a wide variety of protists, algae, plants and invertebrates live in shallow marine to intertidal environments, and virtually all communities from microbial mats to rainforests are tiered. Especially suggestive of a fungal-lichen affinity is preservation as raised compressions resistant to burial compaction. *Dickinsonia* is a locally common fossil and, when found, shows variation in thickness attributable to aerobic decay. Other evidence for aerobic decay during the Neoproterozoic, includes red, highly oxidized palaeosols with isotopically organic carbon yet low organic carbon content (Retallack 2001), fossil actinobacterial fruiting structures (*Primoflagella*: Sokolov & Ivanovski 1990), and fungi (Retallack 1994, Butterfield 2005). Even in Neoproterozoic euxinic black marine phosphorites, fossil embryos show clear evidence of progressive decay (Dornbos & Bottjer 2002). These indications of decay of *Dickinsonia* and other contemporaneous fossils and palaeosols undermine the idea of a fundamentally different regime of Neoproterozoic decay (contrary to Seilacher 1989, Gehling *et al.* 2005). Nor is there any evidence of brittle fracture or fragmentation suggestive of agglutinative skeletons (Seilacher *et al.* 2005), early cementation or microbial death masks (Gehling 1999). Instead, the remarkably deep impressions of *Dickinsonia* were more likely due to a tough biopolymer such as the chitin of fungal cell walls (Retallack 1994). The taphonomy of *Dickinsonia* is comparable not with that of soft bodied jellyfish, worms, and cnidarians, but with the fossil record of fungi and lichens, such as

Thucomyces, *Spongiophyton* and *Prototaxites* (Hallbauer *et al.* 1977, Hueber 2001, Jahren *et al.* 2003). Like fungi and lichens, *Dickinsonia* was firmly attached to its substrate, ground-hugging, moderately flexible, and very resistant to burial compaction. As the largest, toughest and most obvious of the Ediacaran fossils, *Dickinsonia* lichens or mushrooms would have been an important force for global change and metazoan evolutionary radiation during the latest Precambrian (Retallack 1994).

Acknowledgements

References

BEAUMONT, C., QUINLAN, G. & HAMILTON, J., 1988. Orogeny and stratigraphy: numerical models of the Paleozoic in the eastern interior of North America. *Tectonics 7*, 389-416.

BERTRAND-SARFATI, J., MOUSSINE-POUCHKINE, A., AFFATON, P., TROMPETTE, R. & BELLION, Y., 1991. Cover sequences of the West African craton. In *The West African Orogens and Circum-Atlantic Correlatives*, R.D. DALLMEYER & J.P. LECORCHÉ, eds., Springer, Berlin, 65-82.

BRODO, I.M., SHARNOFF, S.D. & SHARNOFF, S., 2001. *Lichens of North America*. Yale University Press, New Haven, CT, xiii + 795 pp.

BRUTON, D.L., 1991. Beach and laboratory experiments with jellyfish *Aurelia* and some remarks on some fossil 'medusoid' traces. In *The Early Evolution of Metazoa and the Significance of Problematic Taxa*, A.B. SIMONETTA & S. CONWAY MORRIS, eds, Cambridge University Press, Cambridge, 125-129.

BUTTERFIELD, N., 2005. Probable Proterozoic fungi. *Paleobiology 31*, 165-182.

CHALONER, W.G., MENSAH, M.K. & CRANE, M.D., 1974. Non-vascular land plants from the Devonian of Ghana. *Palaeontology 17*, 925-947.

CHERNS, L., 1994. A medusoid from the Late Ordovician or Early Silurian of Jemtland, central Sweden. *Journal of Paleontology 68*, 716-721.

CLAPHAM, M.E. & NARBONNE, G.M., 2002. Ediacaran epifaunal tiering. *Geology 30*, 627-630.

CLOUD, P., 1976. The beginnings of biospheric evolution and their biochemical consequences. *Paleobiology 2*, 351-387.

COLLINSON, J.W., ISBELL, J.L., ELLIOTT, D.H., MILLER, M.F. & MILLER, J.M.G., 1994. Permian–Triassic Transantarctic Basin. In *Permian–Triassic Basins and Foldbelts Along the Panthalassan Margin of Gondwanaland*, J.J. VEEVERS & C.M.A. POWELL, eds, *Geological Society of America Memoir 184*, 173-122.

CONAGHAN, P.J., 1980. The Hawkesbury Sandstone. In *A Guide to the Sydney Basin*, C. HERBERT & R. HELBY, eds., *Geological Survey of New South Wales Bulletin 26*, 188-253.

CONWAY MORRIS, S., 1979. Middle Cambrian polychaetes from the Burgess Shale of British Columbia. *Royal Society of London Philosophical Transactions B285*, 227-274.

CONWAY MORRIS, S., PICKERILL, R.K. & HARLAND, T.L., 1982. A possible annelid from the Trenton Limestone (Ordovician) of Quebec, with a review of fossil oligochaetes and other annulate worms. *Canadian Journal of Earth Sciences 19*, 2150-2157.

CRANE, P.R. & DILCHER, D.L., 1984. *Lesqueria*; an early angiosperm fruiting axis from the mid-Cretaceous. *Missouri Botanical Garden Annals 71*, 384-402.

CRAWFORD, E., HERBERT, C., TAYLOR, G., HELBY, R., MORGAN, R. & FERGUSON, J., 1980. Diatremes of the Sydney Basin. In *A Guide to the Sydney Basin*, C. HERBERT & R. HELBY, eds., *Geological Survey of New South Wales Bulletin 26*, 294-323.

DORNBOS, S.Q. & BOTTJER, D.J., 2002. A taphonomic test of the biogenicity of putative phosphatized sponge embryos from the Neoproterozoic Doushantuo Formation, southwest China. *Geological Society of America Abstracts 34*(6), 170.

DOYLE, J.A. & HICKEY, L.J., 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. In *Origin and Early Evolution of Angiosperms*, C.B. BECK, ed., Columbia University Press, New York, 139-208.

DROSER, M.L., GEHLING, J.G. & JENSEN, S., 2003. Voyage to the bottom of the Ediacaran sea; what's missing from the picture? *Abstracts Geological Society of America 35*(6), 106-107.

DROSER, M.L., GEHLING, J.G. & JENSEN, S.R., 2005. Ediacaran trace fossils: true and false. In *Evolving Form and Function: Fossils and Development*, D.E.G. BRIGGS, ed., Peabody Museum of Natural History, Yale University, New Haven, pp. 125-138.

DZIK, J. & IVANTSOV, A.Y., 2002. Internal anatomy of a new Precambrian dickinsoniid dipleurozoan from northern Russia. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte 7*, 385-396.

FEDONKIN, M.A., 1981. Belomorskaya biota Venda (White Sea biota of the Vendian). *Trudy Geologicheskii Instituta Akademia Nauak S.S.S.R 342*, 100 pp.

FEDONKIN, M.A., 1992. Vendian faunas and the early evolution of Metazoa. In *Origin and Early Evolution of the Metazoa*, J.H. LIPPS & P.W. SIGNOR, eds., Plenum, New York, 87-129.

FEDONKIN, M.A., 2002. *Andiva ivantsovi*, gen. et sp. n., and related carapace-bearing Ediacaran fossils from the Vendian of the Winter Coast, White Sea, Russia. *Italian Journal of Zoology 69*, 175-181.

FEDONKIN, M.A., 2003. The origin of the Metazoa in the light of the Proterozoic fossil record. *Paleontological Research, Tokyo 7*, 9-41.

FERGUSON, D.K., 1985. The origin of leaf assemblages—new light on an old problem. *Review of Palaeobotany and Palynology 46*, 117-188.

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.

GAND, G., GARRIC, J., SCHNEIDER, J., SCIAU, J. & WALTER, H., 1996. Biocoenoses à mèduses du Permien Français (Bassin de Saint-Affrique, Massif Central). *Geobios 29*, 379-400.

GEHLING, J.G., 1991. The case for Ediacaran fossil roots to the metazoan tree. *Geological Society of India Memoir 20*, 181-224.

GEHLING, J.G., 1999. Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. *Palaios 14*, 40-57.

GEHLING, J.G., DROSER, M.L., JENSEN, S.R. & RUNNEGAR, B.N., 2005. Ediacara organisms: relating form to function. In *Evolving Form and Function: Fossils and Development*, D.E.G. BRIGGS, ed., Peabody Museum of Natural History, Yale University, New Haven, 43-66.

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., 1994. An enigmatic bilateral fossil from the Lower Cambrian of Morocco. *Journal of Paleontology 68*, 710-716.

GLAESSNER, M.F., 1969. Trace fossils from the Precambrian and basal Cambrian. *Lethaia 2*, 369-393.

GLAESSNER, M.F., 1984. *The Dawn of Animal Life*. Cambridge University Press, Cambridge, xi + 244 pp.

GLAESSNER, M.F. & WADE, M., 1966. The late Precambrian fossils from Ediacara, South Australia. *Palaeontology 9*, 599-628.

GOLDRING, R. & CURNOW, C.N., 1967. The stratigraphy and facies of the Late Precambrian at Ediacara, South Australia. *Geological Society of Australia Journal 14*, 195-214.

GRAZHDANKIN, D., 2004. Patterns of distribution in the Ediacaran biotas: facies versus biogeography and evolution. *Paleobiology 30*, 203-221.

GRAZHDANKIN, D. & SEILACHER, A., 2002. Underground Vendobionta from Namibia. *Palaeontology 45*, 57-78.

HAGADORN, J.W., DOTT, R.H. & DAMROW, D., 2002. Stranded on a Late Cambrian shoreline: medusae from central Wisconsin. *Geology 30*, 147-150.

HALL, J., 1847. *Palaeontology of New York*. State of New York, Albany, 338 pp.

HALLBAUER, D.K. & VAN WARMELO, K.T., 1974. Fossilized plants in thucolite from the Precambrian rocks of the Witwatersrand, South Africa. *Precambrian Research 1*, 199-212.

HALLBAUER, D.K., JAHNS, M.H. & BELTMANN, H.A., 1977. Morphological and anatomical observations on some Precambrian plants from the Witwatersrand, South Africa. *Geologische Rundschau 66*, 477-491.

HARRINGTON, H.J. & MOORE, R.C., 1956. Dipleurozoa. In *Treatise on Invertebrate Paleontology. Part F. Coelenterata*, R.C. MOORE, ed., Geological Society of America and University of Kansas Press, Boulder and Lawrence, F24-F26.

HERBERT, C., 1980. The Wianamatta Group. In *A Guide to the Sydney Basin*, C. HERBERT & R. HELBY, eds, *Geological Survey of New South Wales Bulletin 26*, 254-272.

HINTZE, L.F., 1988. *Geologic History of Utah. Brigham Young University Geology Studies Special Publication 7*, ill + 202 pp.

HOFFMAN, P.F., KAUFMAN, A.J., HALVERSON, G.P. & SCHRAG, D.P., 1998. A Neoproterozoic Snowball Earth. *Science 281*, 1342-1346.

HUEBER, F.M., 2001. Rotted wood-alga-fungus: the history and life of *Prototaxites* Dawson 1859. *Review Palaeobotany Palynology 116*, 123-158.

INGOLD, C.T., 2000. A note about a fairy ring of *Marasmius oreades*. *Mycologist 14*, 33-34.

IVANTSOV, A.Y., 2004. New Proarticulata from the Vendian of the Arkhangel'sk region. *Paleontological Journal 38*, 247-253.

IVANTSOV, A.Y. & FEDONKIN, M.A., 2001. Locomotion trails of the Vendian invertebrates preserved with the producer's body fossils, White Sea, Russia. *PaleoBios Supplement to 21*, 72.

JACKSON, J.B.C. & BUSS, L., 1975. Allelopathy and spatial competition among coral reef invertebrates. *National Academy of Sciences USA Proceedings 72*, 5160-5163.

JAHREN, A.H., PORTER, S. & KUGLITSCH, J.J., 2003. Lichen metabolism identified in Early Devonian terrestrial organisms. *Geology 31*, 99-102.

JENKINS, R.F.J., 1992. Functional and ecological aspects of Ediacaran assemblages. In *Origin and Evolution of the Metazoa*, J.H. LIPPS & P.W. SIGNOR, eds., Plenum Press, New York, 131-176.

JENKINS, R.F.J., 1995. The problems and potential of using animal fossils and trace fossils in terminal Proterozoic biostratigraphy. *Precambrian Research 73*, 51-69.

JENKINS, R.F.J., 1996. Aspects of the geological setting and palaeobiology of the Ediacara assemblage. In *Natural History of the Flinders Ranges*, M. DAVIES, C.R. TWIDALE & M.J. TYLER, eds., Royal Society of South Australia, Adelaide, 33-45.

JENKINS, R.J.F. & GEHLING, J.G., 1978. A review of the frond-like fossils of the Ediacara assemblage. *South Australian Museum Records 17*, 347-359.

JENKINS, R.J.F., FORD, C.H. & GEHLING, J.G., 1983. The Ediacara Member of the Rawnsley Quartzite: the context of the Ediacara assemblage (late Precambrian, Flinders Ranges). *Geological Society of Australia Journal 30*, 101-119.

JURINA, A.L. & KRASSILOV, V.A., 2002. Lichenlike fossils from the Givetian of central Kazahstan. *Paleontological Journal 36*, 100-105.

KENT, L.E., 1980. Stratigraphy of South Africa. Part 1. Lithostratigraphy of the Republic of South Africa, Namibia and the Republics of Baphuthatswana, Transkei and Venda. *South African Geological Survey Handbook 8*, 690 pp.

KIDWELL, S.M. & GYLLENHAAL, E.D., 1998. Symbiosis, competition, and physical disturbance in the growth histories of Pliocene cheilostome bryoliths. *Lethaia 31*, 221-239.

KIRSCHVINK, J., 1992. Late Proterozoic low latitude glaciation. In *The Proterozoic Biosphere*, J.W. SCHOPF, ed., Cambridge University Press, Cambridge, 51-52.

MACRAE, C., 1999. *Life Etched in Stone: Fossils of South Africa*. Geological Society of South Africa, Johannesburg, xiii + 305 pp.

MARTINSSON, A., 1970. Toponomy of trace fossils. In *Trace Fossils*, T.P. CRIMES, ed., *Geological Journal Special Issue 3*, 323-330.

MATTEN, L.C., 1973. Preparation of pyritized plant petrifactions: ' a plea for pyrite'. *Review Palaeobotany Palynology 16*, 165-173.

MCCALLUM, W.S., 1990. Construction material resources, Golden Grove area. *Mines and Energy Review South Australia 1990*, 90-91.

MIHAIL, J.D. & BRUHN, J.N., 2005. Foraging behaviour of *Armillaria* rhizomorph systems. *Mycological Research 109*, 1195-1207.

MOORE, P.S., 1990. Origin of redbeds and variegated sediments, Cambrian–Adelaide Geosyncline, South Australia. *Geological Society of Australia Special Paper 16*, 334-350.

NARBONNE, G.M., 2004. Modular construction of early Ediacaran complex life forms. *Science 305*, 1141-1144.

NIU, S.-W. & SHU, S.-F., 2000. The tentative establishment of Palaeopacific Huainan-Little Dal biogeographic demarcation and its significance; on the palaeontological evidence about reestablishing the Neoproterozoic Rodinia Supercontinent. *Qianhanwuji Yanjiu Jinzhan (Progress in Precambrian Research) 23*, 11-21 (Chinese).

NORRIS, R.D., 1989. Cnidarian taphonomy and affinities of the Ediacara biota. *Lethaia 22*, 381-393.

PARADISE, T.R., 1997. Disparate sandstone weathering beneath lichens, Red Mountain, Arizona. *Geografiska Annaler, Series A, Physical Geography 79*, 177-184.

PETERSON, K.J., WAGGONER, B. & HAGADORN, J.W., 2003. A fungal analog for Newfoundland Ediacaran fossils? *Integrative and Comparative Biology 43*, 127-136.

PFLUG, H.D., 1973. Zur fauna der Nama-Schichten in Südwest Africa. IV. Mikroscopische anatomie der petaloorganism. *Palaeontographica B144*, 166-202.

PFLUG, H.D., 1994. Role of size increase in Precambrian organismic evolution. *Neues Jahrbuch für Geologie Paläontologie Abhandlumgem 193*, 245-286.

POOLE, W.H., SANFORD, B.V., WILLIAMS, H. & KELLEY, O.G., 1976. Geology of southeastern Canada. In *Geology and Economic Minerals of Canada*, R.J.W. DOUGLAS, ed., *Geological Survey of Canada Economic Geology Report 1*, 227-304.

POWARS, D.S. & BRUCE, T.S., 1999. The effects of the Chesapeake Bay Impact Crater on the geological framework and correlation of hydrogeologic units of the lower York-James Peninsula, Virginia. *U.S. Geological Survey Professional Paper 1612*, 82 pp.

RETALLACK, G.J., 1994. Were the Ediacaran fossils lichens? *Paleobiology 20*, 523-544.

RETALLACK, G.J., 1995. Compaction of Devonian lycopsid stems from the Beacon heights Orthoquartzite, southern Victoria Land. *U.S. Antarctic Journal 30*(5), 42-44.

RETALLACK, G.J., 2001. *Soils of the Past*, Blackwell, Oxford, xi + 346 pp.

RETALLACK, G.J., 2004. Soils and global change in the carbon cycle over geological time. In *Treatise on Geochemistry, Volume 5*, H.D. HOLLAND & K.K. TUREKIAN, eds., Elsevier, Amsterdam, 581-605.

RETALLACK, G.J. & DILCHER, D.L., 1981. Early angiosperm reproduction; *Prisca reynoldsii*, gen. et sp. nov. from mid-Cretaceous coastal deposits in Kansas, USA. *Palaeontographica B179*, 103-137.

REX, G.M. & CHALONER, W.G., 1983. The experimental deformation of plant compression fossils. *Palaeontology 26*, 231-252.

RUNNEGAR, B., 1982. Oxygen requirements, biology and phylogenetic significance of the late Precambrian worm *Dickinsonia*, and the evolution of the burrowing habit. *Alcheringa 6*, 223-239.

RUNNEGAR, B., 1992. Evolution of the earliest animals. In *Major Events in the History of Life*, J.W. SCHOPF, ed., Jones and Bartlett, Boston, pp. 65-93.

RUNNEGAR, B., 1995. Vendobionta or Metazoa? Developments in understanding the Ediacaran 'fauna'. *Neues Jahrbuch für Geologie und Paläontologie 195*, 303-318.

SAMUELSON, J., VAN ROY, P. & VECOLI, M., 2001. Micropalaeontology of a Moroccan Ordovician deposit yielding soft-bodied organisms showing Ediacara-like preservation. *Geobios 34*, 365-373.

SCHMIDT, P.W., EMBLETON, B.J.J. & WILLIAMS, G.E., 1993. Early timing of remnance in hematite of the Neoproterozoic Elatina Formation, Adelaide Geosyncline: confirmation of the low latitude of Neoproterozoic glaciation. *Exploration Geophysics 24*, 239-242.

SCHOPF, K.M. & BAUMILLER, T.K., 1998. A biomechanical approach to Ediacaran hypotheses: how to avoid the Garden of Ediacara. *Lethaia 3*, 89-97.

SEILACHER, A., 1989. Vendozoa: organismal construction in the Proterozoic biosphere. *Lethaia 22*, 229-239.

SEILACHER, A., 1992. Vendobionta and Psammocorallia: lost constructions of Precambrian evolution. *Geological Society of London Journal 149*, 607-613.

SEILACHER, A., BUATOIS, L.A. & MANGANO, M.G., 2005. Trace fossils in the Ediacaran–Cambrian transition: behavioral diversification, ecological turnover and environmental shift. *Palaeogeography Palaeoclimatology Palaeoecology 227*, 323-356.

SEILACHER, A., GRAZHDANKIN, D. & LEGOUTA, A., 2003. Ediacaran biota: the dawn of animal life in the shadow of giant protists. *Paleontological Research, Tokyo 7*, 43-54.

SHELDON, N.D. & RETALLACK, G.J., 2001. Equation for compaction of paleosols due to burial. *Geology 29*, 247-250.

SOKOLOV, B.S. & IVANOVSKI, A.B., eds. 1990. *The Vendian System. Vol. 1 Paleontology*, Springer, Berlin, ill + 183 pp.

SPICER, R.A., 1977. The pre-depositional formation of some leaf impressions. *Palaeontology 20*, 907-912.

SPRIGG, R.C., 1947. Early Cambrian (?) jellyfishes from the Flinders Ranges, South Australia. *Royal Society of South Australia Transactions 71*, 212-224.

SPRIGG, R.C., 1949. Early Cambrian 'jellyfishes' of Ediacara, South Australia and Mount John, Kimberley District, Western Australia. *Royal Society of South Australia Transactions 73*, 72-99.

STEIN, W.E., HARMON, G.D. & HUEBER, F.M., 1993. Lichens in the Lower Devonian of North America. *Geological Society of America Abstracts 25*(6), A82.

STEINER, M. & REITNER, J., 2001. Evidence of organic structures in Ediacara-type fossils and associated microbial mats. *Geology 29*, 1119-1122.

STROTHER, P.K., 1988. New species of *Nematothallus* from the Silurian Bloomsburg Formation of Pennsylvania. *Journal of Paleontology 62*, 967-982.

TALLING, P.J., BURBANK, D.W., LAWTON, T.F., HOBBS, R.S. & LUND, S.P., 1994. Magnetostratigraphic chronology of Cretaceous to Eocene thrust belt evolution, central Utah, USA. *Journal of Geology 102*, 181-196.

TAYLOR, J.M., 1950. Pore-space reduction in sandstone. *American Association of Petroleum Geologists Bulletin 34*, 701-706.

TENDAL, O.S., 1972. A monograph of the Xenophyophoria (Rhizopodea, Protozoa). *Galathea Report 12*, 7-99.

TERMIER, H. & TERMIER, G., 1968. *Evolution et biocinése*, Masson, Paris, xii + 241 pp.

VALENTINE, J., 1992. *Dickinsonia* as a polypoid organism. *Paleobiology 18*, 378-382.

WADE, M., 1968. Preservation of soft-bodied animals in Precambrian sandstones at Ediacara, South Australia. *Lethaia 1*, 238-267.

WADE, M., 1972. *Dickinsonia*: polychaete worms from the late Precambrian Ediacara fauna, South Australia. *Queensland Museum Memoir 16*, 171-190.

WEBSTER, M. & HUGHES, N.C., 1999. Compaction-related deformation in Cambrian olenelloid trilobites and its implications for fossil morphometry. *Journal of Paleontology 73*, 355-371.

WILLIAMS, G.E. & SCHMIDT, P.W., 2003. Possible fossil impression in sandstone from the late Palaeoproterozoic–early Mesoproterozoic Semri Group (lower Vindhyan Supergroup), central India. *Alcheringa 27*, 75-76.

XIAO, S., YUAN, X. & KNOLL, A.H., 2000. Eumetazoan fossils in terminal Proterozoic phosphorites? *National Academy of Sciences USA Proceedings 97*, 13684-13689.

YUAN, X., XIAO, S. & TAYLOR, T.N., 2005. Lichen-like symbiosis 600 million years ago. *Science 308*, 1017-1020.

ZHU, M.-Y., ZHAO, Y.-L. & CHEN, J.L., 2002. Revision of the Cambrian discoidal animals *Stellostomites eumorphus* and *Pararotadiscus guizhouensis* from South China. *Geobios 45*, 165-185.

ZHURAVLEV, A.Y., 1993. Were Vend-Ediacaran multicellular Metazoa? *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 190*, 299-314.