Ediacaran characters

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Antcliffe and Hancy (2013) raise questions concerning recent work on Ediacaran fossils (Retallack 2013a), here quoted in full. "What are the characters present in Ediacaran organisms that lead logically to the conclusion that these organisms are the remains of ancient lichens? How was it determined that such characters are unique to lichens to the exclusion of other similar morphological shapes or structures formed by abiological processes? The answers to these questions are not forthcoming." Answers are not forthcoming because they have already been published. Space here permits only a referenced list for *Dickinsonia*, a particularly iconic Ediacaran fossil: (1) unifacial structure, with finished and thick upper surface layer, but less distinct lower surface (Wade 1968, Figs. 17 and 20C; Gehling 1999, Fig. 7); (2) fractal tubular constructional and histological elements (Retallack 2007, Fig. 6); (3) indeterminate isometric growth in width and length to maintain proportions (Retallack 2007, Figs. 3 and 4); (4) indeterminate allometric growth in thickness to maintain ground-hugging form (Retallack 2007, Fig. 3); (5) juvenile thallus unusually large and coarsely plicate compared with adult (Runnegar 1982, Fig. 7); (6) mature growth by radial addition of segments as well as diffuse marginal expansion (Runnegar 1982, Fig. 7); (7) hypothallial rims ("halo margin" of Retallack 2007, Fig. 1A); (8) allelopathic avoidance of other individuals (Retallack 2007, Fig. 1B); (9) fairy ring arrangements of individuals (Retallack 2007, Fig. 1E); (10) greater resistance to burial compaction than comparably scaled fossil tree trunks without any mineral or relict evidence of pyritization (Retallack 2007, Fig. 5); (11) series of decayed individuals showing loss of relief but not of outline (Retallack 2007, Fig. 1E); (12) basal fine rhizine-like extensions down in to matrix (Retallack 2013a, Fig. 2g); (13) attached stout connecting rhizomorphs (Seilacher's "Aulozoon" for Retallack 2007, Fig. 7A); (14) limited marginal overturn and pull apart of thallus over expansion cracks indicating firm cementation or rooting to substrate (Glaessner 1969, Fig. 1E; Retallack 2007, Fig. 1D); (15) growth which effaces primary sedimentary structures such as ripple marks (Xiao 2013, Fig. 1); (16) association with complex microbial surfaces ("old elephant skin" or *Rivularites repertus*) characteristic of desert crusts (Retallack 2012a, Fig. 6A); (17) life position within oxidized, well drained gypsic and calcic paleosols (Retallack 2013a, Fig. 2b); (18) growth through time coordinated with proxies for paleosol development such as proportion of gypsum sand crystals

(Retallack 2013a, Fig. 3). Anticipating Antcliffe and Hancy's (2013) second question, most of these characters are tabulated for comparison with alternative biological affinities by Retallack (2007, Table 5), with the result that lichens and non-lichenized fungus fully (100%) explain 16 characters of *Dickinsonia*, but only 81% are explained by xenophyophores and cnidarian polyps, 75% by cnidarian jellyfish, 69% by polychaete or annelid worms, and 63% by turbellarian worms. The recently proposed idea of *Dickinsonia* as a placozoan (Sperling and Vinther 2010), explains only 50% of the 16 characters of Retallack (2007), and only 28% of the 18 characters listed above.

Antcliffe and Hancy (2013) summon support from Brasier and Antcliffe (2008) for the idea that *Dickinsonia* shrank, and so did not have a rigid or attached carapace. However, the specimen considered unshrunken on the slab with the one considered shrunken by Runnegar (1982) is now known to have been a different species on a different growth trajectory (Retallack 2007). Because both the large and small specimen have a rim of about the same size, it cannot be due to shrinkage of one like the large one to the small one, and is better regarded as a fungal hypothallus, or rim of incomplete hyphal expansion.

Antcliffe and Hancy (2013) leave unspecified the "conclusive evidence that they were marine" from Callow et al. (2013), without citing refutation of that account by Retallack (2013b), who found their marine evidence far from conclusive (ripple marks) or in different beds from the living surfaces of *Dickinsonia* (hummocky cross stratification). Evidence from unusually light carbon and oxygen isotopic composition in outcrop and drill core persuaded Knauth (2013) that the carbonate nodules were pedogenic. Geochemical mass balance showing both volume and common cation loss from the paleosols is most persuasive to me, as it cannot form during sedimentation in which titanium-bearing heavy minerals drop to the bottom of a bed (Retallack 2012b). Also compelling is evidence from distinctive complex associated mats formed by a highly deviatoric system of shrinking, swelling, overgrowth, and healing (Retallack 2012a). Other features of the paleosols with *Dickinsonia* include downward gradational destruction of bedding, drab-haloed filament traces (*Prasinema gracile*), soil crust pedestals, loess-like grain size and fabric, replacive (not displacive) sand crystals and nodules of calcite, and gypsum at characteristic depth below bed tops, desiccation cracks, ice heave and melt structures, needle ice impressions, red redeposited soil clasts in gray fluvial sandstones, and red colour

of rocks with illitic-sericitic Ediacaran-style weathering and metamorphism rather than unmetamorphosed bauxitic and kaolinitic deep weathering (Retallack 2012b, 2013a). Although the foregoing data apply to the type Ediacaran fossil beds of South Australia, a new round of work on Newfoundland Ediacaran localities is revealing both paleosols and very shallow marine paleoenvironments there as well (Retallack 2012c, 2013c). Despite Antcliffe and Hancy's (2013) rallying cry that "we should not be distracted by false debates about terrestrial sediments," marine versus terrestrial nature of these deposits is a real and testable scientific question of direct relevance to the nature of these genuinely enigmatic fossils.

The phylogenetic placement of Ediacaran fossils does not need to be a Rorschach test of everything that remotely looks like them, as portrayed by Antcliffe and Hancy (2013, Fig. 1). Evidence, not just appearance, will be needed to solve this puzzle. The picture matching approach was emphatically not the reason for my suggestion of lichen affinities. *Dickinsonia* has a passing similarity to foliose lichens such as *Xanthoparmelia*, and my 20 years of searching has found very rare specimens in which the normally radial symmetry is elongated along twigs or cracks in rock or soil to bestow a superficial resemblance to *Dickinsonia*, but none that have the apparent regularity of form of *Dickinsonia*. The lichen hypothesis was instead based on measurements of burial compaction of the fossils indicating that they had a biopolymer more resistant to compaction than lignin, thus suggesting chitin of fungi and lichens (Retallack 1994). Subsequent observations confirmed that *Dickinsonia* was sessile and grew firmly attached to its substrate (Retallack 2007), and lived in low nutrient coastal aridland soils (Retallack 2013a). Although *Dickinsonia* may not look exactly like any particular modern lichen, it does seem to have shared their mechanical strength, lifestyle, and habitats.

Lichens are placed phylogenetically within Fungi, not algae, nor cyanobacteria of their phycobiont, and current understanding of fungal phylogeny makes ascomycotan or basidiomycotan affinities of Ediacaran fossils unlikely (Berbee and Taylor 2010). Permineralized fragments of glomeromycotan lichens have now been found in Ediacaran rocks as old as 600 Ma (Yuan et al. 2005), but their overall form remains uncertain for comparison with Ediacaran fossils. Endosymbiotic Glomeromycota may have a fossil record extending back 1480 Ma (Retallack et al. 2013a), or perhaps 2200 Ma (Retallack et al. 2013b). Vendobionta like *Dickinsonia* were an extinct group whose precise phylogenetic placement has yet to be determined by future discovery of preserved histology and reproductive structures (Retallack 2007), and are best considered fundamen-

tally fungal until proven otherwise. The museum catalog of the Museum of Natural and Cultural History of the University of Oregon provisionally includes Vendobionta as an extinct Class within Glomeromycota.

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