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Megafossils from the Ediacaran Period (635–541 Ma) have been controversial in part because many are mere impressions in coarse-grained rocks. New examination of these fossils in petrographic thin-sections reveals various features that inform understanding of the biological affinities of these problematic fossils. Material examined includes *Dickinsonia costata* from the Ediacara Member of the Rawnsley Quartzite in South Australia, *Ernietta plateauensis* from the Kliphoek Member of Namibia, *Ivesheadia lobata* from the Drook Formation of Newfoundland, *Charnia antecedens* and *Charniodiscus spinosus* from the Mistaken Point Formation of Newfoundland, *Aspidella terranovica* from the Fermeuse Formation of Newfoundland, and *Nemiana simplex* from the Mogilev Formation of Ukraine and the Verkovka Formation of Russia. Three characteristics stand out for all but *Nemiana*. First, these fossils were remarkably resistant to burial compaction, as originally inferred from depth gauge measurements of overlying moulds, and here confirmed by thin-sections perpendicular to bedding planes. Second, thin-sections reveal a construction of micrometric branching elongate structures forming millimetric hollow elongate structures in fractal arrangements. Third, some of the fossils are asymmetric bifacial or unifacial, with a thick finished upper wall but lower wall thin or non-existent and attached to elongate structures downward into sediment. Compaction-resistant fossils with asymmetric histological layering are most like crustose and fruticose lichens fortified with chitin. In contrast, non-resistant impressions in the tops of beds filled by overlying cross-bedded sediment, as in *Nemiana*, preserve no informative histology and are similar to lake balls and microbial colonies.

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MUCH CONFUSION concerning fossils of the Ediacaran Period is due to poor preservation as impressions in coarse-grained sandstone of the original South Australian examples (Wade 1968, Retallack 1994, 2007, Gehling 1999). Laser scanning (Brasier & Antcliffe 2009), computer-assisted retrodeformation (Gehling & Narbonne 2007, Hofmann *et al*. 2008), and associated microfossils (Retallack 2015a) have improved our understanding of these fossils, but Ediacaran impression fossils remain a kind of Rorschach test when it comes to proposing biological affinities (Antcliffe & Hancy 2013a). Proposed affinities of large Ediacaran impression fossils have been all over the tree of life: tunicates (Fedonkin *et al*. 2012), arthropods (Lin *et al*. 2006), molluscs (Gehling *et al*. 2014), worms (Runnegar 1982, Dzik & Ivantsov 2002, Dzik & Martyshyn 2015), placozoans (Sperling & Vinther 2010), echinoderms (Gehling 1987), ctenophores (Zhang & Reitner 2006), scyphozoans (Wade 1968, Jenkins 1992, Valentine 1992), sponges (Gehling & Rigby 1996), stem group metazoans (Grazhdankin 2014), fungi (Retallack 1994, 2007, 2013a, 2014b, 2015a, Peterson *et al*. 2003), foraminifera (Seilacher 1989, 1992, Seilacher *et al*. 2003), algae (Ford 1958), or separate extinct kingdoms Vendozoa (Seilacher 1989) or Vendobionta (Seilacher 1992). There are also studies concluding that the distinctive quilted Ediacaran fossils could not have been sea pens (Antcliffe & Brasier 2007), corals (Retallack 2007), placozoans (Retallack 2013a), worms (Seilacher 1989), jellyfish (Seilacher 1989), fungi (Antcliffe & Hancy 2013a, b), foraminifera (Antcliffe *et al*. 2011) or algae (Retallack 1994, 2007). Likely habitats of Ediacaran fossils also have proven controversial and varied: deep ocean (Narbonne 2005, Narbonne *et al*. 2014), to outer continental shelf (Grazhdankin 2004), nearshore marine (Gehling 2000, Weaver *et al*. 2006, Aceñolaza 2012, Gehling & Droser 2013, Retallack 2014c), intertidal zone (Jenkins *et al*. 1983, Retallack 2014b, 2016a), coastal plains (Retallack 2012, 2013a, 2014b, 2016a) and river floodplains (Kolesnikov *et al*. 2012, Barroso *et al*. 2014). Marine habitats were inferred as a consequence of interpretation of the fossils as marine invertebrates (Wade 1968, Runnegar 1982, Jenkins 1992, Valentine 1992), which can no longer be assumed (Retallack 1994, 2007, Antcliffe & Brasier 2007, Antcliffe *et al*. 2011). Marine palaeoenvironments rest largely on field photographs of turbidites and hummocky cross-stratification, whose relationship with the fossils is unspecified (Callow *et al*. 2012, Antcliffe & Hancy 2013b, Narbonne *et al*. 2014, Retallack 2016a). Evidence from stable isotopes, C/S ratios, Fe_{HR}/Fe_T and mass balance geochemistry suggests a mix of coastal shallow marine, intertidal and terrestrial habitats (Retallack 2013a, b, 2014a, b, 2016a).

There is widespread agreement that most Ediacaran fossils were sessile creatures, living and growing on the sediments in which they are found (Gehling 1999, Narbonne 2005, Hofmann *et al.* 2008, Gehling & Droser 2013, Retallack, 2013a, 2014b, 2016b). The few large Ediacaran fossils considered as evidence of loco-motion (Ivantsov & Malakhovskaya 2002, Menon *et al.* 2013) could instead have been multiple individuals (Retallack 2007) or growth rugae of sessile individuals (Retallack 2014d). Other supposed rasping traces (Gehling *et al.* 2014) might instead be fish-tail twins of gypsum or ground ice needles (Retallack 2013a). Most Ediacaran trail-like impressions were made by smaller and different organisms than the large fossils (Liu *et al.* 2010, Chen *et al.* 2013, Carbone & Narbonne 2014, Meyer *et al.* 2014a, MacDonald *et al.* 2014), and some are misinterpreted tool marks (Retallack 2010) or trails of aggregated amoebozoans in the 'slug' (grex) phase (Retallack 2013c).

A useful approach to understanding Ediacaran fos-sils in growth position is petrographic study of the fossils in their enclosing rocks (Pflug 1973, 1994, Jenkins *et al.* 1978, Xiao *et al.* 2005, Laflamme *et al.* 2011, Retallack 2013a, Meyer *et al.* 2014b). The classi-cal South Australian fossils have not been helpful in this respect, because most of them are upper external moulds (concave hyporelief) in which the matrix is the unrelated overlying sandstone (Fig. 1). The fidelity of the impression in some external moulds is enhanced by films of iron oxide, perhaps from iron-oxidizing bacte-ria, such as *Sphaerotilus*, known to encrust modern (Spicer 1977) and Cretaceous leaves (Retallack & Dilcher 2012). Less common are South Australian counterpart specimens of the rock in which the fossils grew (Fig. 2B, Gehling 1999, Retallack 2007, 2013a). Other Ediacaran fossils from Newfoundland and the Russian White Sea are permineralized and nodularized in pyrite (Dzik & Ivantsov 2002, Retallack 2014b), though not encrusting 'pyritic death masks' (Gehling 1999). Yet others from Namibia are permineralized in ferruginous silica (Pflug 1973, 1994). This array of impressions and permineralization is comparable with preservation of fossil plants, and pyritized or silicified plants are especially informative about histology and thus biological affinities (Matten 1973, Spicer 1977, Tidwell & Jones 1987). This study describes several Ediacaran fossils in thin-section and uses that informa-tion to constrain their biological affinities. Unlike earlier petrographic studies of Ediacaran fossils, all the thin-sections reported here were oriented and cut vertical to regional bedding. In the cases of *Dickinsonia*, *Charniodiscus* and *Charnia*, the thin-sections illustrated here are the first reported for those genera.

Material and methods

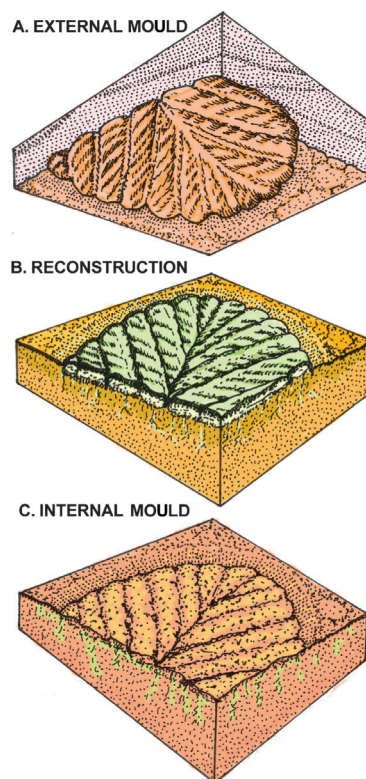Petrographic materials of Ediacaran fossils have been difficult to obtain because of special legal protection of

Fig. 1. Ediacaran fossil *Dickinsonia costata*, as preserved in the Ediacara Member of the Rawnsley Quartzite in the Flinders Ranges. **A**, Common upper external mould or concave hyporelief; **B**, Recon-struction; **C**, Less commonly collected lower internal mould or convex epirelief. Transverse wrinkles to the main ribs are based on observa-tions of large specimens (Retallack 2007) and serial photography mod-elling (Brasier & Antcliffe 2008), but are often smoothed out in reconstructions as animals (Runnegar 1982, Seilacher 1989, 2007).

the fossils and their fossil sites. Specimens described here are in the collections of the Condon Collection of the Museum of Natural and Cultural History of the University of Oregon, and predate legislative gazetting in Newfoundland or under permit from South Australian National Parks (Fig. 2). Most were obtained within pet-rographic thin-sections made for the purpose of palaeoenvironmental study (Retallack 2013a, 2014b). In those cases, the thin-sections were assigned to taxa seen at the edges of the slabs in low diversity assemblages at the same localities (Narbonne *et al.* 2005, Retallack 2013a). Thin-sections were mostly from specimens marked for orientation when collected in the field, and cut vertical to bedding planes.

Material examined includes *Dickinsonia costata* from the Ediacara Member of the Rawnsley Quartzite in the Ediacara Hills, Brachina Gorge and Hookapunna Well, South Australia (collected by Retallack 1994, 2007, 2013a). These fossils are atop massive and nodular red beds interpreted as wave-base sands by Gehling & Droser (2013), but as aridland palaeosols by Retallack (2012, 2013a). These deposits are upper Ediacaran and corre-spond to the LELP acritarch Zone (late Ediacaran Leiosphere Palynozone of Gaucher & Sprechmann 2009) and dated to 550 Ma (age model of Retallack 2013a).
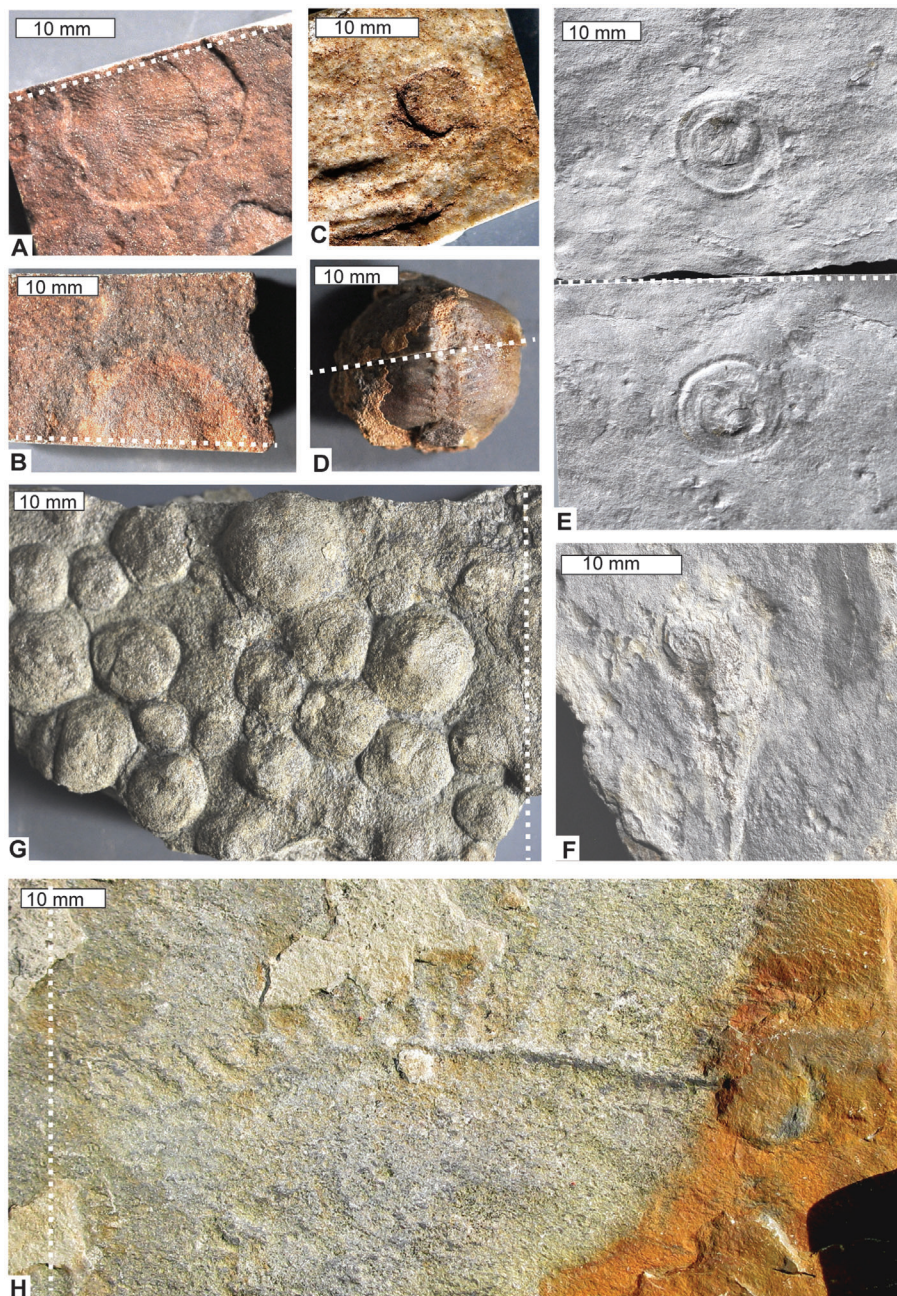
Fig. 2. Ediacaran megafossils. **A**, External mould of upper surface of *Dickinsonia costata* from the Ediacara Member of the Rawnsley Quartzite in the Ediacara Hills, South Australia; **B**, Internal mould of lower surface of *Dickinsonia* sp. from Hookapunna Well, South Australia; **C–D**, External mould of compression (**C**) and silicified cast of individual (**D**) of *Ernietta plateauensis* from the Kliphoek Member of the Dabis Formation, near Aus, Namibia; **E–F**, Part and counterpart (**E**) and stalked individual (**F**) of *Aspidella terranovica* from the Fermeuse Formation of Ferryland (south locality), Newfoundland; **G**, Sole markings of *Nemiana simplex* from the Yampol Member of the Mogilev Formation, Novodneistrov power house, Ukraine; **H**, Frond of *Charniodiscus spinosus* from the Mistaken Point Formation at Green Head, Newfoundland. Dashed white lines show position of cuts for thin-sections made. Specimen numbers in the Condon Collection of the Museum of Natural and Cultural History of the University of Oregon are (A) F112999A, (B) F115186, (C) F113776, (D) F113777, (E) F116742A& B, (F) F116744, (G) F115668A, (H) F116714.

Ernietta plateauensis from the Kliphoek Member of the Dabis Formation, near Aus, Namibia, was collected by Pflug (1966, 1972). These specimens were recovered from float, but specimens in growth position elsewhere in Namibia were interpreted as living in intertidal to shallow marine shoreface sands by Dzik (1999). These specimens of *Ernietta* are also in the late Ediacaran LELP acritarch Zone (Germs *et al*. 1986, Gaucher &

Sprechmann 2009), and about 550 Ma by local radiometric dating (Meyer *et al*. 2014b).

Charniodiscus spinosus and *Charnia antecedens* are both from the Mistaken Point Formation, at the Newfoundland localities of Green Head and west of St Shotts, respectively (Retallack 2014b). These fossils are interpreted as growing on top of deep sea turbidites by Narbonne (2005), but on grey sulfidic intertidal

palaeosols by Retallack (2014b, 2016a). The Mistaken Point Formation is in the Ediacaran Complex Acanthomorph Palynoflora Zone of Grey (2005) and dated using zircon U–Pb at 565.0 ± 3 Ma at Mistaken Point (van Kranendonk *et al.* 2008).

Ivesheadia lobata is from the Drook Formation, at Pigeon Cove, Newfoundland (Retallack 2014b), from the same surface described as a deep sea turbidite by Liu *et al.* (2012). This bed has been reinterpreted as the surface of an intertidal pyritic palaeosol of the Murphys pedotype by Retallack (2014b, 2016a). A tuff immediately overlying this surface has been dated by zircon U–Pb at 578.8 ± 0.5 Ma (van Kranendonk *et al.* 2008), and remains ungraded with gas escape structures as if deposited on land (Retallack 2014b).

Aspidella terranovica from the Fermeuse Formation of Newfoundland can be found in road cuts near Ferryland, but more informative material studied here was found in the less weathered shore platform of Freshwater Cove, 2 km to the south (Retallack 2014c). Their sedimentary setting has been considered prodeltaic (Gehling *et al.* 2000), but the specimens studied here were collected from intertidal, grey, pyritic palaeosols (Retallack 2014c). In the age model of Retallack (2014b), these are about 560 Ma in age.

Nemiana simplex was examined from the Verkhovka Formation of the White Sea coast, Russia (Grazhdankin 2004, Leonov 2007), and from the Yampol Member, Mogilev Formation near Novodneistrov power station, Podolia, west-central Ukraine (Fedonkin & Vickers-Rich 2007). Both are in the late Ediacaran range of Kotlin-Rovno assemblages (Vidal & Moczydłowska-Vidal 1997), equivalent to the LELP acritarch Zone (Gaucher & Sprechmann 2009). The Russian specimens are from deltaic distributary mouth bar sandstone facies (Grazhdankin 2004), and Ukrainian specimens from comparable planar laminated sandstones (Grazhdankin *et al.* 2011). From the U–Pb zircon ages compiled by Grazhdankin (2014), the Russian examples are equidistant in the section between levels dated at 555.3 and 558.0 Ma, and the Ukrainian fossils are not much older than 553 Ma old.

Petrographic observations

Dickinsonia costata

Thin-sections of *Dickinsonia costata* (Fig. 2A–B) confirm the compaction-resistant preservation and striking difference in clarity of upper and lower surfaces (Fig. 1), as first noted by Wade (1968). The thick and smooth upper surface of the fossil juts up into overlying cross-bedded sandstone (concave hyporelief), but the lower surface is a less well defined network of near vertical elongate structures (convex epirelief: Fig. 3A). These are resistant fossils in the sense of Wade (1968) and raised impressions of Retallack (1994). Cross-bedding is clear in the overlying sand-

stone, but bedding in the underlying sandstone is disrupted by wispy, near-vertical extensions of red ferruginized clay (Fig. 3B, C). Indistinct lower internal moulds (Fig. 2B) also show lack of bedding and common subvertical wisps of ferruginous clay (Fig. 3D).

Ferruginous clay is thick and lumpy on the uppermost surface, but below that is a broadly chambered structure including some silt-sized grains. The grainy interior has a wispy horizontal division, and also scattered vertical divisions corresponding in scale (1–2 mm) to ribs evident in the fossil impressions. Irregularities of cross-struts support observations of large specimens by Retallack (2007), and serial photographic modelling of Brasier & Antcliffe (2008), which indicate transverse wrinkling of the ribs (Fig. 1). Wrinkles are usually smoothed out in artistic restorations of *Dickinsonia* as an animal (Runnegar 1982, Seilacher 1989, 2007).

Also at shallow depths below *Dickinsonia* are large, subhorizontally elongate, hollow structures, filled with siltstone and lined with ferruginous clay (Fig. 3A). These are the strap-shaped fossils referred to 'Aulozoon' (*nomen nudum*) by Seilacher *et al.* (2003). All four *Dickinsonia* on one large slab in the South Australian Museum are over the ends of 'Aulozoon' (Retallack 2007), suggesting a relationship between the two, here confirmed by two additional associations in thin-section.

Ernietta plateauensis

Available specimens of *Ernietta plateauensis* (Fig. 2C–D) did not include permineralized histology like that documented by Pflug (1973). The specimens examined for this study are mostly silicified three-dimensional sandstone moulds (Figs 2B, 4). One specimen (Fig. 2C) is a flattened impression protruding into cover sandstone, like the preservation of *Dickinsonia*. The three-dimensional moulds not only are filled with sand on the inside but preserve two wall layers separated by cross-partitions between open areas with internal siltstone grains (Fig. 4A–E). Thus, the ribs visible on the outside are internal hollow structures. The inner wall appears thinner and more diffuse than the outer wall, although the outer one is incompletely preserved (best shown in Fig. 4A bottom). The inner wall also has wispy extensions into the interior where it forms a diffuse mesh of ferruginized films well dispersed in the sandstone matrix (Fig. 4D, E).

Ivesheadia lobata

The 'pizza disc' fossil *Iveheadia lobata* is permineralized thoroughly in pyrite, which accentuates the opacity of original organic matter, and contrasts with grey silty clay of the matrix (Fig. 5D, E). The body is asymmetric, with elongate structures extending down into the matrix further than short upward projections. These elongate structures are near vertical near the top
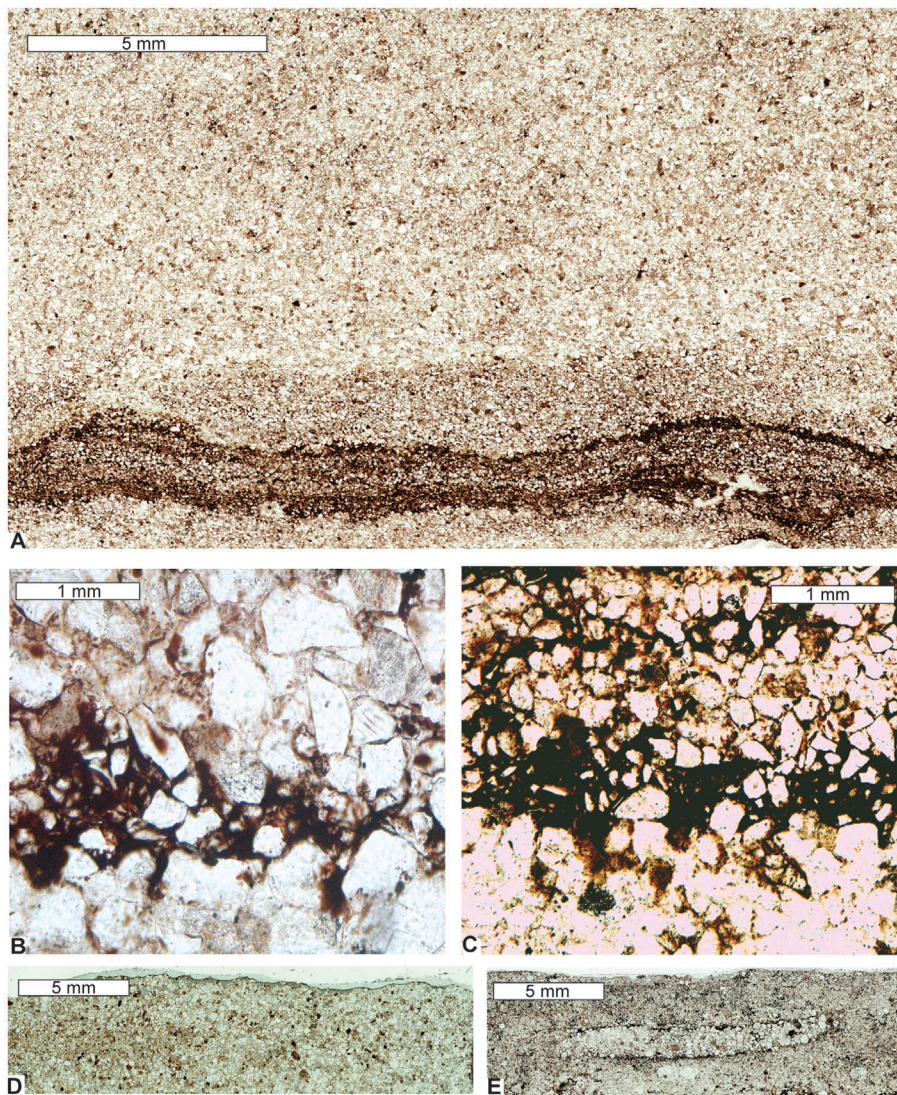
Fig. 3. Petrographic thin-sections cut vertical to bedding of *Dickinsonia costata* (**A–D**) and '*Aulozoon*' (**E**) from the Ediacara Member of the Rawnsley Quartzite. **A–C, E**, from Brachina Gorge; **D**, from near Hookapunna Well, in South Australia, and from Muru (**A, E**), and Warrutu (**B, C**) pedotypes of Retallack (2013a). Specimen numbers in the Museum of Natural and Cultural History of the University of Oregon are (A) F1179737, (B, C) F117936A, (D) F115736, (E) F115735.

and bottom, but are interwoven like spaghetti in the middle. Unlike elongate wispy structures seen in all the other thin-sections, these elongate structures are parallel sided and maintain a constant width to a rounded end. Furthermore, they include quartz and other silicates indicating that they were hollow tubes about 10–20 μm in diameter. There are clear upper and lower opaque walls to the whole structure, and also scattered rounded interior chambers filled with clay (Fig. 5E). These clay-filled chambers are clumped at intervals of 10–15 mm along the width of the body. Between these internal chambers, pyrite and organic matter are opaque but with vertical struts separating the upper and lower wall. Projections from the base of the structure are less well oriented but generally are directed downward (Fig. 5D).

Charnia antecedens

Charnia antecedens has a strongly asymmetrical body from top to bottom, with a thick pyrite-organic upper wall that curves around one edge, then thins toward the middle part of the lower surface of the body (Fig. 5C). The upper wall is thick within areas that correspond to quilt islands on the fossil. Between this thick upper wall and the thin lower wall are areas filled with clay, but the inner surface of both walls is diffuse. The lower wall boundary is also diffuse and extends downward in elongate, wispy extensions. This specimen appears partly dismembered (to the right), and this tear might have enabled penetration of silt into internal spaces. The clarity of the lower wall also decreases to the right, as if it were partly decayed.
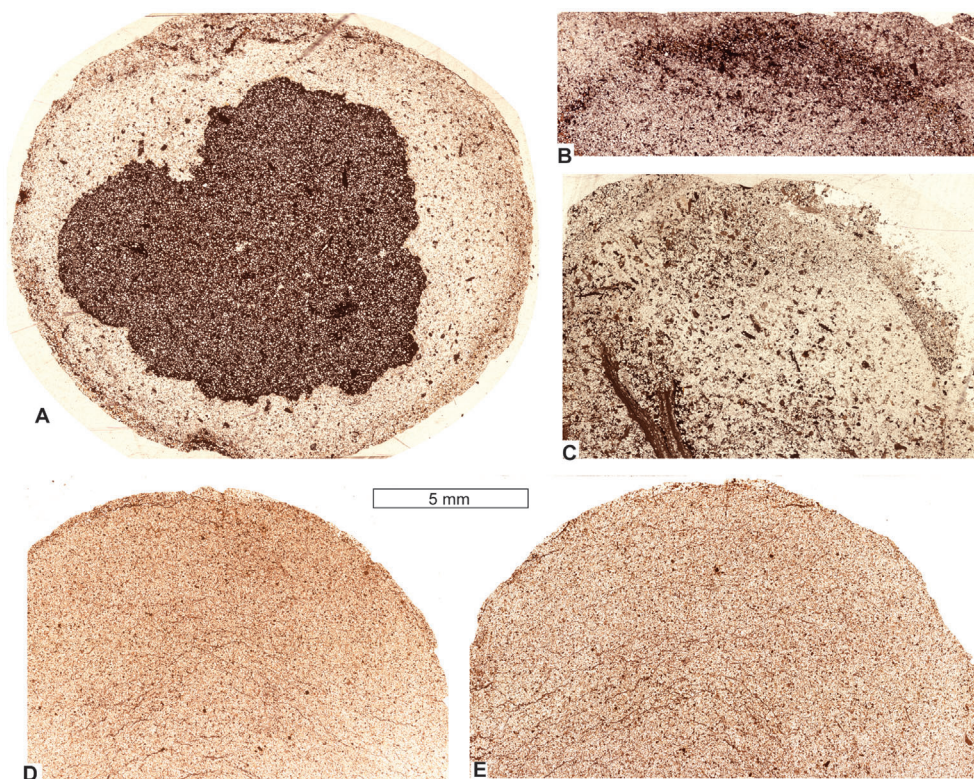
Fig. 4. Petrographic thin-sections cut vertical to bedding of *Ernietta plateauensis* Kliphoek Member of the Dabis Formation, Aus, Namibia. Specimen numbers in the Museum of Natural and Cultural History of the University of Oregon are (A) F113782, (B) F113781, (C) F113779, (D) F113785, (E) F113787.

Charniodiscus spinosus

A frond of *Charniodiscus spinosus* (Fig. 2H) is preserved by pyrite permineralization within an 8-mm-thick silty layer atop grey shale (Fig. 5A). The frond has a complex fractal tubular structure, whereby the central hollow axis has been infiltrated by silt and sand, and there are similar complex tubular structures both above and below this prone axis (Fig. 5A). The walls of fine (0.5–0.8 mm diameter) tubules are opaque, with rounded framboids of pyrite in chains between wispy outer and inner walls (Fig. 5B). In thin-sections (Fig. 5B) of second-order ribs of Laflamme *et al.* (2004), walls are strongly sinuous, reflecting higher orders of branching, comparable with the complex fractal branching structure described for other Ediacaran fronds (Narbonne *et al.* 2009)

Aspidella terranovica

Aspidella terranovica is a compaction-resistant fossil in the sense of Wade (1968), but commonly preserved as carbonaceous lenses (Fig. 6A, B) in shaley siltstone rather than sandstone. The uppermost wall is thick and opaque and bulges up from the bedding plane (Fig. 6C–F). Below that are open spaces with included grains, and a thin lower wall, which dissolves into elongate wispy structures penetrating the sediment below. Some of these extensions are organized into large

conical structures (Fig. 2F), which are ptygmatically folded owing to burial compaction (Fig. 6B). These larger structures have also been found in megafossils, and were considered stalks of fronds that extended upward out of the sediment (Gehling *et al.* 2000, Menon *et al.* 2013). Such inferences could only be made from unoriented specimens, because specimens collected in place from outcrops and marked for orientation as a part of this study showed that these ptygmatically folded, elongate structures tapered strongly downward into the sediment below *Aspidella* (Fig. 6B). Organic structures in thin-sections of *Aspidella* were interpreted by Laflamme *et al.* (2011) as microbial mats, but the lenticular organic masses interpreted as *Aspidella* here lack the lamination of mats. Laflamme *et al.* (2011) regarded associated sandstone ripples and load casts as *Aspidella*, but they have relief almost an order of magnitude greater than *Aspidella* observed on slabs.

Nemiana simplex

Nemiana simplex is a non-resistant fossil in the sense of Wade (1968), because the fossil collapsed with decay or burial compaction into the depression on laterally displaced substrate. This hole was then filled in with cross-bedded sand from above (Fig. 7). The organic material of the fossil, which makes such a clear sole impression (Fig. 2G), is thus reduced to such a thin film that few histological details are visible. Wisps of
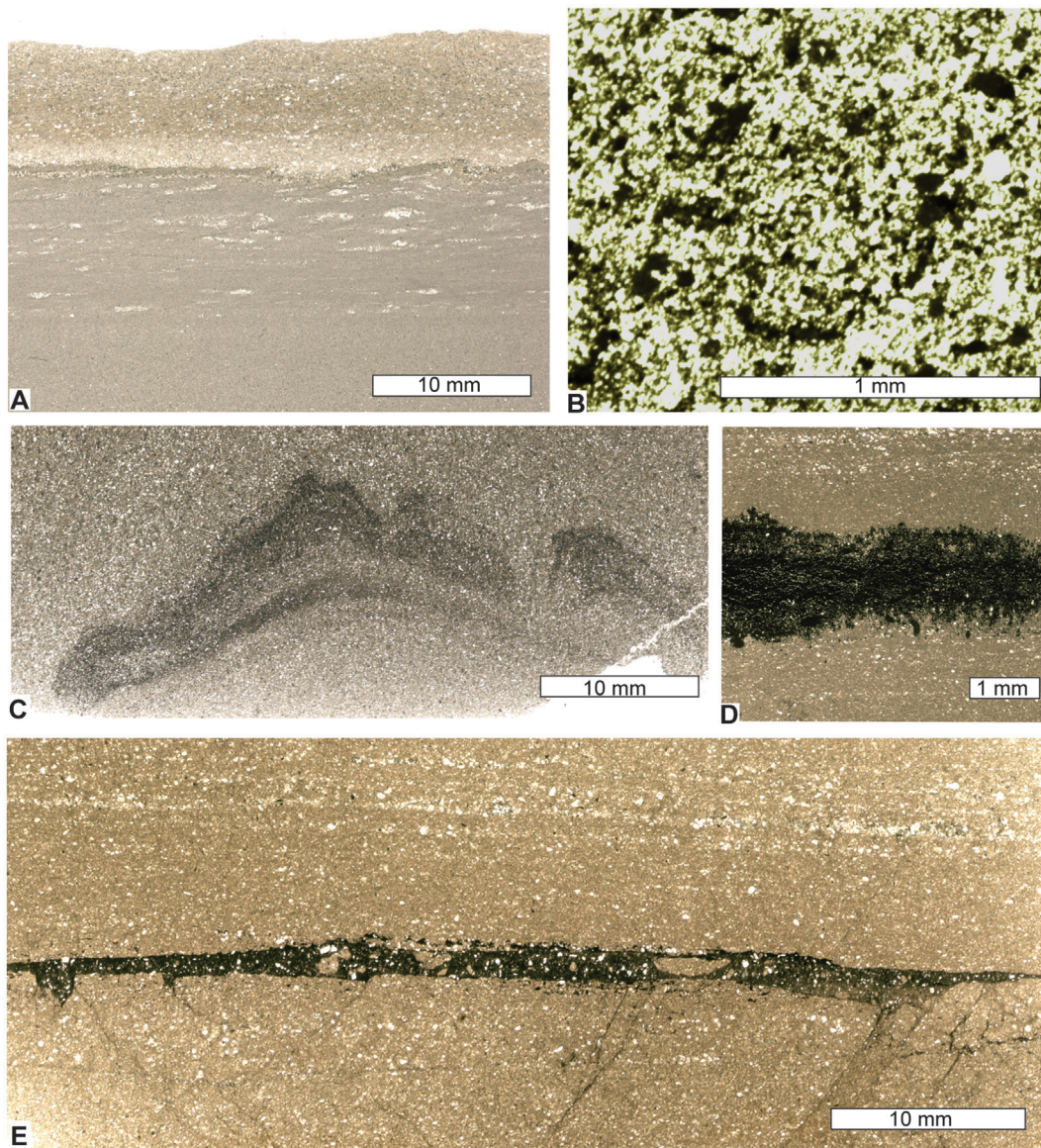
Fig. 5. Petrographic thin-sections cut vertical to bedding of Ediacaran fossils from Newfoundland. **A–B**, *Charniodiscus spinosus*; **C**, *Charnia antecedens*; **D–E** *Ivesheadia lobata* from the Mistaken Point Formation of Green Head (**A–B**) and St Shotts (**C**) and Drook Formation of Pigeon Cove (**D–E**). Specimen numbers in the Condon Collection, Museum of Natural and Cultural History of the University of Oregon are (A, B) F116714, (C) F117932, (D) F117935, (E) F117934.

opaque organic matter extend a short distance into the overlying sandstone (Fig. 7). The relief of the lower side of the fossil is nevertheless preserved by the less compactable sand fill on a more clayey substrate, as commonly observed in trace fossil concave hyporeliefs (Seilacher 2007).

Ediacaran taphonomy

Various preservational styles are represented in the material studied here, and these preservational styles are well known among Phanerozoic fossils (Retallack 2011b). The most faithful preservation of histology is in pyrite permineralizations (*Charnia, Charniodiscus, Ivesheadia*), followed by carbonaceous compressions (*Aspidella*), and then ferruginized moulds and casts (*Dickinsonia, Erniettia*). Pyrite permineralization is pervasive through the organic part of both fossils and associated organic mats or crusts, but no examples of a pyritized rind to an unpyritized fossil are known (Dzik & Martyshyn 2015, Retallack 2016a), leaving the theoretical 'death mask' model of Gehling (1999) without an example. Quality of histological preservation varies in the pyritized fossils examined, best in *Ivesheadia* and worst in *Charnia*. Such a range of preservation is comparable with that in pyritized fossil plants, which may have faithfully pyritized tracheids but obliterated pyritized parenchyma (Matten 1973). These pyritized fossils are the only ones with potential for histological preservation, because cell structure has been compacted beyond recognition in carbonaceous compressions and largely oxidized in ferruginized moulds and casts. Nevertheless, wispy partitions of carbon and haematite
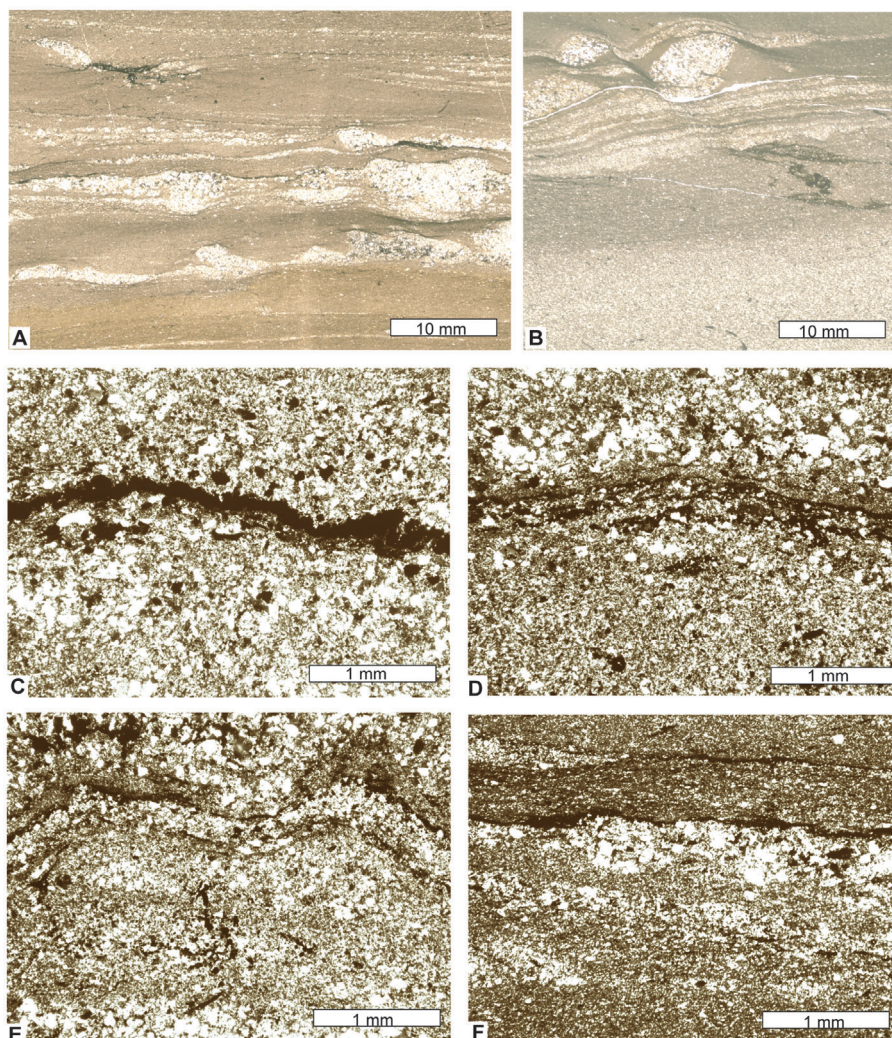
Fig 6. Petrographic thin-sections cut vertical to bedding of *Aspidella terranovica* Fermeuse Formation, Freshwater Cove, Newfoundland. Specimen numbers in the Condon Collection, Museum of Natural and Cultural History of the University of Oregon are (A, F) F116749, (B) F116754A, (C) F116771, (D) F116770A (E) F116771.

do reflect structural boundaries, comparable with carbonaceous and ferruginized moulds and casts of chambered plant fossils, such as *Artisia* (Falcon-Lang 2003) and *Equisetites* (Kelber 2015).

Ediacaran histology

Terminology

Pflug (1970a, b, 1972, 1973, 1994) pioneered histological study of Ediacaran megafossils, and some of his non-genetic terminology remains useful. The whole body was called a petalode (petalodium). At the smallest scale, petalodes are constructed of tubules (tubulae), which are filamentous cells some 1–5 μm in diameter (Fig. 8A). These tubules are linked laterally into sheets defining larger (1–3 mm) hollow tubes (tubae) or ribs (Rippen), which in thin-section appear like internal hollows, in some cases invaded by sediment. The ribs are derived by alternate branching from an axial and original rib or tube, which is below the central groove (fossa medialis) in *Dickinsonia* and *Ernietta*. This central tube, from which others branch, is developed into a much larger hollow axis (centrarium) in frondose fossils, such as *Charniodiscus*. In the frondose fossils, the lateral linkage of ribs develops multiple orders of branching, which can be described as first- through fourth-order ribs, from largest to smallest.

Pflug's (1973) histological terminology was reviewed by Retallack (1994), who found that each of his terms has equivalents in terminology for lichens, including prosplectenchyma (Endogewebe), pseudoparenchyma (Ectogewebe), hypha (tubula), podetium (tuba or Rippen), soredium (globulus, cupulus), soralium (cupulae Aggregat) and pruina (Karbonat Kristall). The terminology for lichens also works well for current histological observations (Fig. 8C), explaining thick upper wall (upper cortex), chambered interior (medulla and algal layer), thin lower wall (lower cortex, absent in crustose lichens) and basal wispy extensions (rhizines).
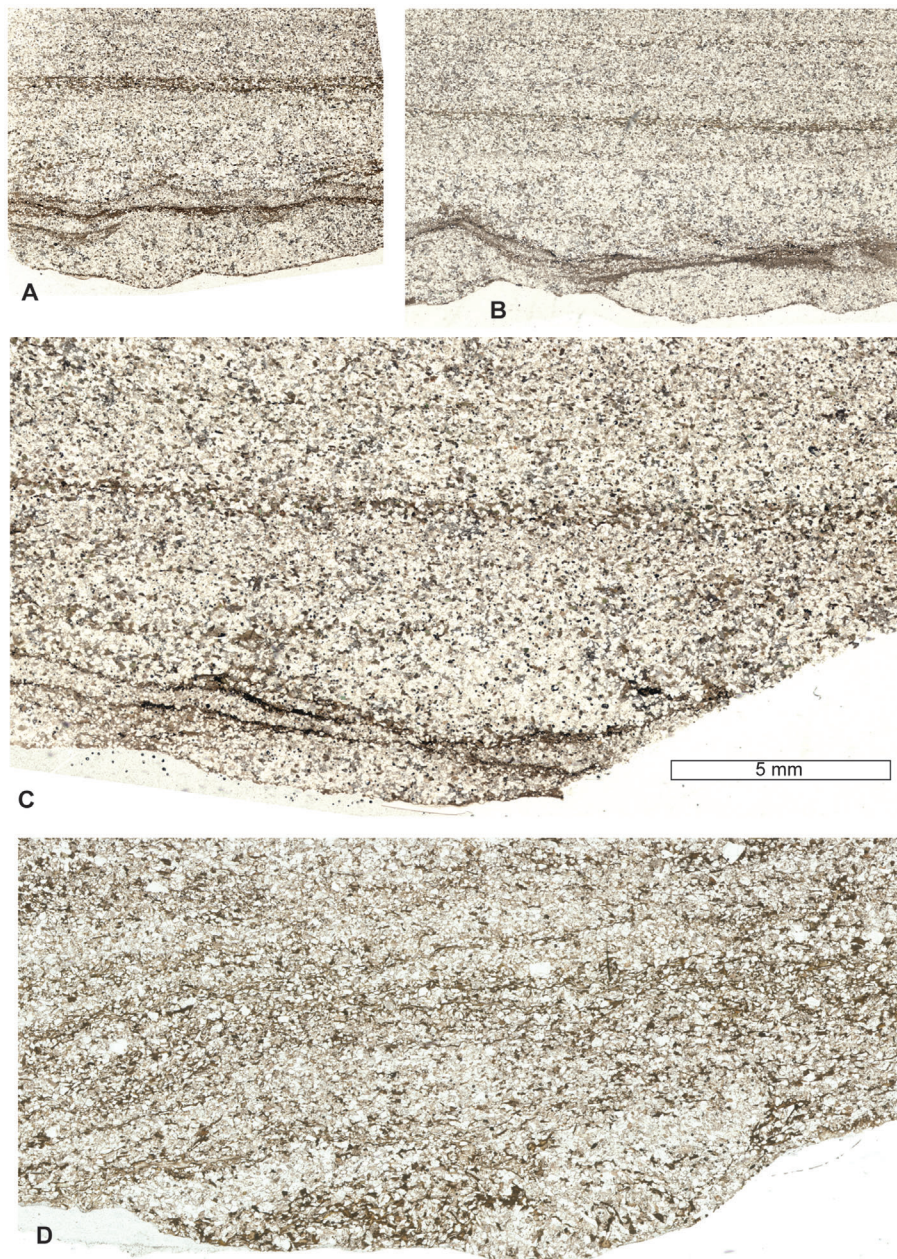
Fig. 7. Petrographic thin-sections cut vertical to bedding of *Nemiana simplex*: **A–C**, from the Verkhovka Formation, White Sea coast, Russia; **D**, from the Yampol Member, Mogilev Formation, Novodneistrov power station, Ukraine. Specimen number in the Museum of Paleontology, University of California at Berkeley is (A–C) 10297, and in the Condon Collection, Natural and Cultural History of the University of Oregon is (D) F115777.

Vendobionta were defined by Seilacher (1992, p. 607) as follows:

> Immobile foliate organisms of diverse geometries that were only a few millimetres thick, but reached several decimetres in size. A shared characteristic is the serial or fractal quilting of the flexible body wall, which stabilized shape, maximized external surface and compartmentalized the living content.

These quilts were termed 'pneu structures' (Fig. 8B) by Seilacher (1989), with the implication that their shape was maintained by interior pressure of water or air. The high relief of fossils demonstrated here, despite local tearing (Figs 3A, 4A, 5C, 6E), makes hydrostatic support unlikely. A compaction-resistant biopolymer, such as chitin, has long been invoked (Fedonkin 1990, Retallack 1994) for those Ediacaran fossils that bulge above their substrate. The pneu structures are generally termed ribs (Pflug 1994), but Seilacher's term 'quilted' remains an apt description of the segments, and has been clearly demonstrated for *Yangtziramulus* (Xiao *et al.* 2005, Shen *et al.* 2009). This terminology does not work for non-quilted and non-resistant Ediacaran fossils, such as *Nemiana* (Figs 2G, 7), which were very different kinds of organisms (MacGabhann 2007).
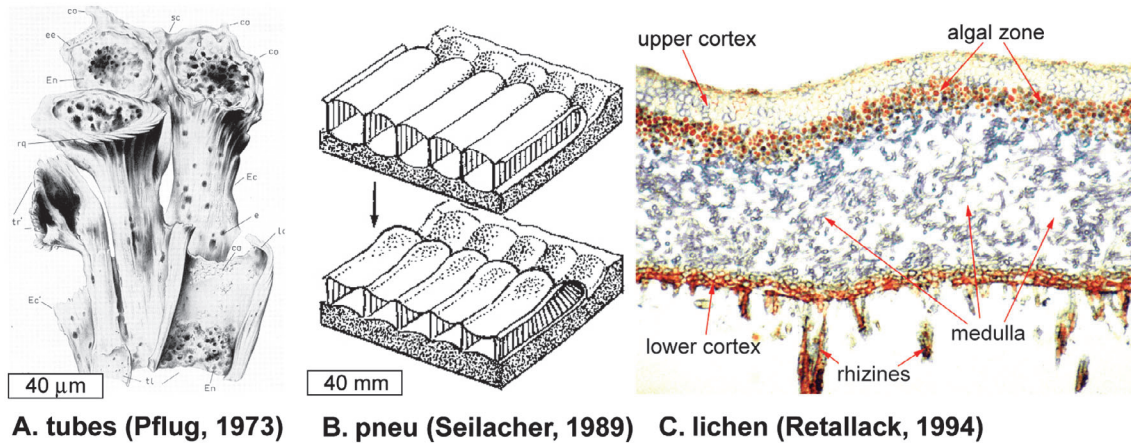
A. tubes (Pflug, 1973)   B. pneu (Seilacher, 1989)   C. lichen (Retallack, 1994)

Fig. 8. Past histological interpretations of Ediacaran fossils: **A**, from Pflug (1973); **B**, from Seilacher (1989); **C**, cross-section of lichen *Physcia aipolia* from George Barron, with permission.

Wall asymmetry

A distinctive feature of many of the fossils examined is asymmetric development of walls: thick outer and upper wall, above internal spaces, then a thin inner and lower wall fading into wispy downward extensions. In some cases (*Dickinsonia, Ernietta, Charnia, Ivesheadia*), this can be described as asymmetric bifacial: the interior spaces separate an upper thick from a lower thin wall with lower extensions. In other cases (*Aspidella*), the structure can be described as unifacial, with an upper wall prominent but lower surface of mainly downward extensions. Other walls are very complexly folded and branched (*Charniodiscus*), or not adequately preserved (*Nemiana*).

Internal chambers

Internal chambers between the thick upper and thin lower walls of *Charnia, Dickinsonia, Ernietta* and *Ivesheadia* are not as clearly defined as the outside ribbing of these genera (Fig. 2), or the pneu model (Fig. 8B) of Seilacher (1989). Cross-partitions are slender compared with upper and lower walls, and some partitions are partly disrupted. One way to interpret such irregularities is as a sequence of decay, in which cells are dislodged from the regular structure as their supportive tissue rots. If this were true, the irregularity would increase as opacity of organic matter declined. However, the most organic and opaque specimens (*Ivesheadia*, Fig. 5E) have the most irregular cavities, and heavily ferruginized, but organic lean specimens (*Dickinsonia*, Fig. 3A) have regular cross-struts between the walls. Furthermore, *Dickinsonia* cross-sections have retained thickness unlike other decayed specimens, which have deflated and lost structure (Retallack 2007). These observations support the less organized tube structure proposed by Pflug (1973) and the lichen model of Retallack (1994), over the pneu structure of Seilacher (1989) for vendobionts (Fig. 8).

Other systems of axial chambers interpreted as intestines, caecae and gonads have been proposed for longitudinally folded impression specimens of *Dickinsonia* (Dzik & Ivantsov 2002) and the similar *Podolimurus* (Dzik & Martyshyn 2015). Wrinkled specimens of *Dickinsonia* are well known and have been contrasted with the usual rigid fossils (Evans *et al.* 2015), perhaps stiffened by desiccation (Retallack 2016b). Although wrinkles are real, and rare in impressions, no differentiated sediment-filled passageways for such internal organs were seen in any of the thin-sections for this study.

Cell shape

A striking feature of all the thin-sections of Ediacaran fossils examined is the lack of isodiametric cubic to rectangular cells, of the sort called parenchyma or palisades in plant anatomy (Taylor *et al.* 2009) or epithelium of animals (Ushatinskaya & Parkhaev 2005). Spherical cells are clear in silica permineralized specimens, both enclosed within filamentous cells, or floating within a mesh of tubes (Pflug 1973, 1994), but these were unclear in the thin-sections examined here. This study instead found various wispy elongate or tubular structures arranged into sheets of varying thickness or as individual extensions penetrating the substrate to the fossils (Fig. 9). Differences between the permineralized histology of Pflug (1973, 1994), and the indistinct structures observed in thin-section can be attributed to decay and compression. In the specimens examined here, the pyrite permineralized *Ivesheadia* (Fig. 5D, E) had the best preservation of cellular structure.

Homologous forms

Thick coherent upper and thin irregular lower walls, as in *Dickinsonia*, were also seen in *Charnia* and *Ivesheadia* (Fig. 9). Such a structure in *Charnia* is surprising because it is often reconstructed as an erect

frond (Narbonne *et al.* 2014), in which case continuous thick outer walls and sheaths like those observed here in *Charniodiscus* fronds would be expected (Laflamme *et al.* 2004). Observations of its asymmetric thallus here (Fig. 5C) suggest that *Charnia* might have been a substrate-hugging form like *Dickinsonia*. The holdfasts of *Charnia* and several other comparable frondose forms (Table 1) are either small or absent, and their central stems are flimsy without a load-bearing taper (Sun 1986, Boynton & Carney 2003, Narbonne & Gehling 2003, Laflamme *et al.* 2007, Gehling & Narbonne 2007, Flude & Narbonne 2008, Bamforth *et al.* 2008, Brasier & Antcliffe 2009, Bamforth & Narbonne 2009, Narbonne *et al.* 2009), unlike erect fronds, such as *Charniodiscus* (Laflamme *et al.* 2004), *Rangea* (Grazhdankin & Seilacher 2005), *Swartpuntia* (Narbonne *et al.* 1997), *Parviscopa* and *Primocandelabrum* (Hofmann *et al.* 2008). Additional evidence that some frondose fossils, such as *Trepassia*, were recliners is preservation for considerable lengths (2 m) under very thin tuffaceous cover beds without overfolding or fragmentation (Laflamme *et al.* 2012).

The wall layers and organization of *Ernietta* are similar to those of *Dickinsonia*, but upside down and cup-shaped, as indicated by *Ernietta* bases in life position (Dzik 1999), and by redeposited whole specimens (Ivantsov *et al.* 2016). Wall layers and orientation of *Ernietta* are also similar to those of *Pteridinium* (Pflug 1970a, Grazhdankin & Seilacher 2002, Meyer *et al.* 2014b), *Arumberia* (Kumar & Pandey 2008, 2009, Kolesnikov *et al.* 2012) and *Phyllozoon* (Jenkins & Gehling 1978, Retallack 2007). These taxa appear to have lived partly buried in sediment (Dzik 1999, Grazhdankin & Seilacher 2002).

Observations of *Aspidella* as a compaction-resistant unifacial quilted fossil (Fig. 6) support the restricted definition of *Aspidella* advocated by MacGabhann (2007). Contrary to Gehling *et al.* (2000), it was not the holdfast of a frondose form like *Charniodiscus* (Laflamme *et al.* 2004), because no large hollow stems were seen comparable with those documented by Tarhan *et al.* (2010). Nor was it a non-resistant discoid or medusoid form like *Spriggia* or *Ediacaria* (Gehling *et al.* 2000). The type material of *Aspidella* and allied taxa (Table 1) differs from these concentrically and radially ribbed forms by a small area of ribbing within the center (Fig. 2E). *Spriggia*, *Ediacaria*, *Medusinites* and many other discoid forms are preserved as convex hyporeliefs on the soles of overlying beds (Wade 1968, 1969, Retallack 1994, MacGabhann 2007), like *Nemiana* studied here. Finally, *Aspidella* had small and large elongate extensions down into the substrate (Fig. 6). Undulations considered evidence of movement (spreiten) of *Aspidella* by Menon *et al.* (2013) were more likely growth rugae (Retallack 2014c).

Biological affinities

Foraminifera

Vendobionts have been regarded as xenophyophore foraminifera (Seilacher 1989, 1992, Seilacher *et al.* 2003), but the chambered and asymmetric petalodes studied here are nothing like chambered tests of foraminifera, because they lack initial chambers (proloculae), wall perforations and helical or serial chamber sequences (Antcliffe *et al.* 2011). All the fossils studied here appear to have been variably ferruginized or pyritized organic structures that were compaction resistant, yet somewhat pliable (Seilacher 1989, Gehling *et al.* 2000, Laflamme *et al.* 2004, Fedonkin & Vickers-Rich 2007, Retallack 2007, Liu *et al.* 2012). None had a brittle calcareous, or agglutinated skeleton characteristic of foraminifera (Antcliffe *et al.* 2011). Wispy downward extensions of Ediacaran fossils (Figs 3–6) are more substantial than pseudopodia of foraminifera.

Algae

Fronds of *Charnia* were originally considered to be brown algae (Ford 1958). Various algal compressions, including brown (Phaeophyta), green (Chlorophyta), and red (Rhodophyta) algae, are now known from the Ediacaran (Xiao *et al.* 2002) and, like Phanerozoic fossil algae, are preserved as flattened carbonaceous thalli (Taylor *et al.* 2009), like *Nemiana* (Fig. 7), but very different from the compaction-resistant vendobionts studied here. Algae can be preserved in three dimensions if mineralized by carbonate or permineralized by phosphate, but they also have tissues distinct from those seen here: elongate radiating cells in Chlorophyta and Phaeophyta, and cubic cells in Rhodophyta (Taylor *et al.* 2009).

Animals

Initially, Ediacaran fossils were interpreted as marine invertebrates (Wade 1968, Runnegar 1982, Jenkins 1992, Valentine 1992), and similar interpretations persist (Zhang & Reitner 2006, Sperling & Vinther 2010, Grazhdankin 2014, Gehling *et al.* 2014, Dzik & Martyshyn 2015). Doubt was first cast on such affinities by Seilacher (1989, 1992), who indicated that the supposed worms had neither guts nor metameric segments, nor true bilateral symmetry, and supposed jellyfish had little marginal musculature. Another insightful observation against animal affinities was demonstration that supposed Ediacaran sea pens grew by apical addition rather than basal expansion (Antcliffe & Brasier 2007). The main objection to animal interpretation from the present study is their compaction resistance, despite the lack of a mineralized skeleton (Retallack 1994). This same requirement for a tough structural biopolymer makes it

Order	Definition	Preservation	Temporal range	Geographic range	Constituent genera
Dickinsoniamorpha	Asymmetric bifacial walls in compaction-resistant bipolar petalode	Raised impressions	Cryogenian–Silurian (840–433 Ma)	Liulaobei Formation of China, Mistaken Point, Trepassey and Fermeuse formations of Newfoundland; Lamtsa, Verkhovka, Zimnegory and Erga formations of Russia; Yaryshev Formation of Ukraine, Blueflower Formation of NW Canada; Ediacara Member and Grindstone Range Sandstone of South Australia; Shawangunk Formation of New Jersey	*Andiva, Dickinsonia, Fractifusus, Rutgersella, Windermeria*
Erniettomorpha	Asymmetric bifacial walls with inner rhizomorphs in compaction-resistant bipolar petalodes living within sediment	Internal moulds and raised impressions	Middle Ediacaran–middle Cambrian (560–500 Ma)	June Beds and Blueflower Formation of NW Canada; Sonia and Maihar sandstones of India; Kliphoek and Nasep members of Namibia; Verkhovka and Erga formations of N. Russia; Krutikha and Zigan formations of Uralian Russia; Arumbera Sandstone and Central Mount Stuart Formation of Northern Territory; Floyd Church Formation of North Carolina; Shibantan Member of China; Bonney Sandstone and Moodlatana Formation of South Australia	*Arumberia, Ernietta, Erytholus, Mialsemia, Namalia, Nasepia, Palaeoplatoda, Phyllozoon, Protechiurus, Pteridinium, Yangtziramulus, Valdainia, Ventogyrus*
Charniomorpha	Symmetric bifacial walls and basal rhizomorphs in compaction-resistant unipolar frondose petalodes	Internal moulds and raised impressions	Mid–late Ediacaran (580–560 Ma)	Drook, Mistaken Point, Trepassey and Fermeuse formations of Newfoundland; Beacon Hill and Bradgate formations of England; June beds of NW Canada; Ediacara Member of South Australia; Shibantan Member of China	*Charnia, Cyanorus, Beothukis, Bradgatia, Frondophyllas, Hapsidophyllas, Ivovicia, Paracharnia, Thectardis, Trepassia, Vaisitzinia*
Rangeomorpha	Symmetric bifacial walls in compaction-resistant unipolar and multivaned frondose petalode with stalk and holdfast with rhizomorphs	Internal moulds and raised impressions	Middle Ediacaran – Devonian (580–483 Ma)	Mistaken Point, Trepassey and Fermeuse formations of Newfoundland; June Beds, Sheepbed and Blueflower formations of NW Canada; Verkhovka, Zimnegory and Erga formations of Russia; Khatyshpyt Formation of Siberia; Kliphoek and Spitzkopf members of Namibia; Cid Formation of North Carolina; Ediacara Member and Uratanna Formation of South Australia; Wood Canyon and Poleta formations of California; Moscow Formation of New York	*Avalofractus, Archaeaspinus, Charniodiscus, Culmofrons, Epibaon, Kharakhtia, Lossina, Marywadea, Onega, Pambikalbae, Paravendia, Pectinifrons, Praecambridium, Primocandelabrum, Protonympha, Rangea, Spriggina Swartpuntia, Vendia, Vendomia, Yorgia*
Aspidellomorpha	Asymmetric unifacial walls and basal rhizomorphs in compaction-resistant discoid petalode	Raised impressions	Cryogenian–Ordovician (770–484 Ma)	Kurgan Formation of Kazakhstan; Ives Head Formation of England; Drook, Mistaken Point, Trepassey, Fermeuse and Renews Head formations of Newfoundland; Sonia Sandstone of India; June Beds and Ingta Formation of NW Canada; Erga, Verkhovka and Zimnegory formations of Russia; Cid Formation of North Carolina; Ediacara Member and Grindstone Range Sandstone of South Australia	*Albumares, Anfesta, Arkarua, Aspidella, Conomedusites, Hallidayia, Hiemalora, Ivesheadia, Kimberella, Parvancorina, Solza, Skinnera, Temnoxa, Tribrachidium, Triflorellina*

Table 1. Suggested orders of Class Vendobionta. References to ranges include Johnson & Fox (1968), Wade (1969), Sun (1986), Niu (1997), Narbonne *et al.* (1997), Jensen *et al.* (1998), Hagadorn *et al.* (2000), Grazhdankin & Seilacher (2002, 2005), Grazhdankin (2004, 2014), Boynton & Carney (2003), Laflamme *et al.* (2004, 2012), Xiao *et al.* (2005), Conway Morris & Grazhdankin (2006), Weaver *et al.* (2006), Fedonkin & Vickers-Rich (2007), Flude & Narbonne (2008), Bamforth *et al.* (2008), Hofmann *et al.* (2008), Kumar & Pandey (2008, 2009), Bamforth & Narbonne (2009), Retallack (2009, 2011a, 2013a, 2014b), Meert *et al.* (2011), Kolesnikov *et al.* (2012), Narbonne *et al.* (2014).

unlikely that concave hyporeliefs of *Dickinsonia* were ctenophores (Zhang & Reitner 2006) or placozoans (Sperling & Vinther 2010). For the same reason, *Kimberella* was probably not a slug-like mollusc (Gehling *et al.* 2014), nor were *Tribrachidium, Skinnera* or *Parvancorina* 'stem group metazoans' (Grazhdankin 2014). Contrary to Grazhdankin's (2014) view of *Nemiana* as a 'psammocoral' is the observation here of sedimentary fill of substrate cavities left by a highly compacted body (Fig. 7). No sediment-filled cavities were found comparable with imagined intestines, caecae or gonads (Dzik & Ivantsov 2002, Dzik & Martyshyn 2015). Finally, Seilacher's (1992) orthogonal chambers of *Dickinsonia* were confirmed in thin-section, rather than tubular chambers required for such a large animal to respire (Gooden 2014).

Fungi including lichens

Interpretation of vendobionts as fungi was initially based on their compaction-resistant concave hyporeliefs attributed to chitin, and the histological zonation of filaments and tubules (Retallack 1994, 2007), similar to lichens (Figs 8C, 9). Additional indications of fungal affinities came from fractal branching morphology, lognormal size distribution indicative of indeterminate growth and lack of any visible organs of assimilation, suggestive of diffuse osmotrophy. These arguments of Peterson *et al.* (2003) stopped short of suggesting lichenized fungi because of presumed deep marine habitats, well below the photic zone. This objection is now removed by discovery of vendobionts in formerly well-drained palaeosols in both South Australia (Retallack 2012, 2013a) and Newfoundland (Retallack, 2014b, 2016a). Thin-sections of '*Aulozoon*' (Fig. 3E)

associated with *Dickinsonia* (Retallack 2007) support the observations of Seilacher *et al.* (2003) that it was a hollow tube rather than a burrow, and comparable with fungal rhizomorphs (Retallack 2007).

Fungal and lichen interpretation of Ediacaran fossils was dismissed by Antcliffe & Hancy (2013a, b), who claimed that Ediacaran fossils are interbedded with multiple levels of hummocky cross-stratification indicative of shallow marine to shoreface environments. However, only two examples of hummocky cross-stratification in Ediacaran formations have been documented to date, and neither has associated fossils: (1) the Ediacara Member of the Rawnsley Quartzite at Red Range, South Australia (Gehling 2000, fig. 10d); (2) the Murphys Cove Member of the Mistaken Point Formation near Catalina, Newfoundland (Retallack 2014b, fig. 4F). Objections to fungal affinities by Antcliffe & Hancy (2013b) are based on denial of the following observations: (1) asymmetric unifacial or bifacial structure of Ediacaran fossils (Retallack 2013a, fig. 2c–g: also here in Figs 3–6); (2) fractal branching of frondose vendobionts (Narbonne *et al.* 2009, Cuthill & Conway Morris 2014; also here Fig. 2H); (3) marginal halo comparable with hypothallial rims (Retallack 2007, fig. 1A,6; also here Fig. 2A, B); (4) circlets of fossils comparable with 'fairy rings' of mushrooms (Retallack 2007, fig. E; Ivantsov & Malakhovskaya 2002, figs 1–2); (5) greater resistance to compaction than fossil trees (Retallack 1994, fig. 4, Retallack 2007, fig. 5); (6) attached fine rhizomorphs (Retallack 2013a, fig. 2c–g: also here Figs 3–6); and (7) attached stout rhizomorphs (Retallack 2014c, fig. 1B, C; also here Figs 2F, 6B). These features may be unfamiliar, but are uniquely shared by lichens.

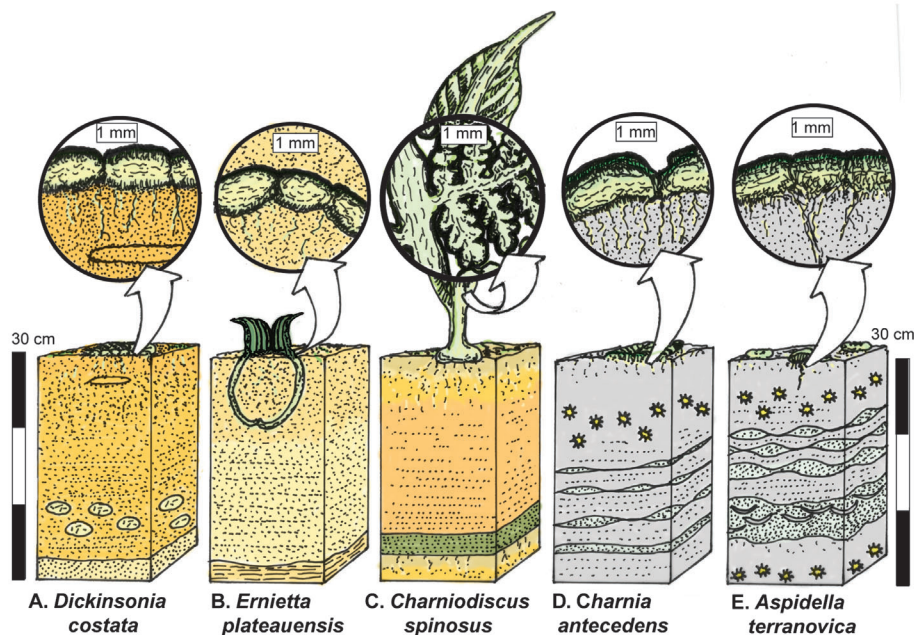*Fig. 9.* Reconstructions of Ediacaran fossils, their histology and palaeosols (after Retallack, 2013a, 2014b).

A. *Dickinsonia costata*   B. *Ernietta plateauensis*   C. *Charniodiscus spinosus*   D. *Charnia antecedens*   E. *Aspidella terranovica*

Another objection to the interpretation as lichens is: how could fronds maintain themselves erect in air without vascular tissues? Ediacaran frond fossils are no larger than modern morels and mushrooms, which have chitinous hyphae, almost as strong as lignin tracheids, and much stronger than cellulose cell walls of plants (Retallack 1994). Mushrooms reach 1 m tall (Wood & Thomas 1989), and podetiate lichens 18 cm tall (Brodo et al. 2001). Trunks of the extinct Devonian lichen *Prototaxites loganii* reached 22 m tall (Retallack & Landing 2014), but these had secondary growth rings not seen in thin-sections of Ediacaran fossils. Some Ediacaran fronds were thick and star shaped in cross-section (Jenkins 1985) with a tapering stalk (Laflamme et al. 2004, 2007), like that of *Prototaxites* considered adapted for load bearing (Retallack & Landing 2014), and unlike the flexuous bases of marine macroalgae (Harder et al. 2006).

Recent support for the idea that *Fractofusus-Charniodiscus* communities of Newfoundland included lichens is additional documentation of palaeosols (Retallack 2014b, 2016a), evidence of nutrient uptake from their substrate (Antcliffe et al. 2015), surrounding small asexual propagules (Mitchell et al. 2015), and limited connectivity more like terrestrial rather than aquatic communities (Mitchell 2015).

Microbial colonies

Discoidal Ediacaran fossils, such as *Nemiana* (Figs 2G, 7), have a very different histology and preservational style, and are termed convex hyporeliefs by Seilacher (2007), non-resistant fossils by Wade (1968), sunken impressions by Retallack (1994), and gravity casts by MacGabhann (2007). Although traditionally regarded as jellyfish (medusoids of Wade 1968), such an explanation is incompatible with this form of preservation on bed soles (MacGabhann 2007) and with anatomical details of the fossils (Seilacher 1989). Ediacaran discoidal fossils might have been rolled aggregates, comparable with lake balls of green algae such, as *Cladophora* (Kindle 1934), and of ditch grass *Ruppia maritima* (Essig 1948), or microbial colonies comparable with biofilm clusters of Proteobacteria, such as *Pseudomonas* (Stoodley et al. 1999), aggregates of myxobacteria, such as *Chondromyces* (Steiner & Reitner 2001), 'mares eggs' of the cyanobacterium *Nostoc* (Dodds & Castenholz 1988), or concentric rings of cyanobacteria, such as *Oscillatoria* (Gerdes et al. 1993, Grazhdankin & Gerdes 2007). Gelatinous lichens, such as *Collema* are also a possibility because they are soft with an abundance of cyanobacteria, such as *Nostoc* (McCune & Rosentreter 2007, Wedin et al. 2009). Although *Nemiana* studied here (Figs 2G, 7) looks like lake balls, modern examples are usually larger, up to the size of watermelons (Essig 1948), and *Cladophora* balls may show radial filaments (Kindle 1934), not seen in *Nemiana*. *Nemiana* also lacks the concentric growth rings of oscillatoriacean cyanobacterial colonies (Gerdes et al. 1993), and is larger than proteobacterial clusters (Stoodley et al. 1999). Nostocalean 'mares eggs' have a thin trichomatous rind prone to wrinkling around a gel interior, small surface bumps and attached colony initials (Dodds & Castenholz 1988), all seen in various specimens of *Nemiana* illustrated by Leonov (2007). Conclusive evidence for biological affinities of discoidal fossils requires microscopic information that is seldom preserved (MacGabhann 2007).

Higher taxonomy

The histological similarities between the Ediacaran fossils and lichens discussed here make it more likely that Vendobionta belonged within Kingdom Fungi, rather than an independent kingdom of life envisaged by Seilacher (1992). No fungal spores of Basidiomycota or Ascomycota have been found older than Devonian, and some acritarchs associated with Ediacaran fossils are very similar in form, ultrastructure and biochemistry to chlamydospores and vesicles of the fungal phylum Glomeromycota (Retallack 2015a). Other evidence for non-dikaryan fungi (Glomeromycota and Mucoromycotina) is now known as far back as the Palaeoproterozoic (Yuan et al. 2005, Retallack et al. 2013a, b, 2014a). Thus, a phylum rank for extinct groups of vendobionts is also unlikely, although Petalonamae was proposed as a phylum by Pflug (1972) for a limited array of these fossils. Whatever the affinities of Vendobionta, it is best regarded as a taxon with the rank of class (if these are considered lichens then note that lichens are classified according to their fungal component). Most of the families proposed by Pflug (1970a, b, 1972, 1973) and orders of Erwin et al. (2011) thus remain valid within Class Vendobionta. My suggested ordinal classification (Table 1) takes the view that these fossils were lichenized fungi, and that histological organization and mode of growth of their petalodes are more important to their classification than symmetry.

Table 1 also includes various vendobionts of ages other than Ediacaran. Some of these date back to the Cryogenian (Niu 1997, Meert et al. 2011), whereas others persisted past the late Ediacaran extinction of most vendiobionts (Johnson & Fox 1968, Jensen et al. 1998, Hagadorn et al. 2000, Retallack 2009, 2011a, 2015b), into rocks as young as Devonian (Conway Morris & Grazhdankin 2005, 2006). Both the Cryogenian and Devonian fossils are controversial, and currently under re-examination. Table 1 does not include the plausible vendobionts *Thaumaptilon* from the Burgess Shale of Canada or *Emmonsapsis* from the Parker Slate of Vermont (Conway Morris 1993), which are preserved as non-resistant carbonaceous compressions, more like macroalgae (Xiao et al. 2002), than vendobionts (Retallack 1994, 2007). Vendobionta were, thus, not limited to the Ediacaran Period.

Vendobionts were not the only Ediacaran fossils. The classification (Table 1) and inference of fungal affinities advocated here applies only to compaction-resistant quilted Ediacaran megafossils (Vendobionta of Seilacher 1992), and does not apply to the great range of other Ediacaran fossils, including: (1) non-resistant discoids (microbial colonies), such as *Nemiana* (Fedonkin & Vickers-Rich 2007, Grazhdankin *et al.* 2012); (2) non-resistant flexuous carbonaceous compressions (sea weeds), such as *Doushantouphyton* (Xiao *et al.* 2002); (3) calcareous stromatolites (cyanobacteria), such as *Tungussia* (Walter *et al.* 1979); (4) calcified cyanobacteria, such as *Girvanella* (Riding 2006); (5) chitinous tubes (scyphozoans?), such as *Corumbella* (Warren *et al.* 2012); (6) calcareous tubes (serpulid worms?), such as *Cloudina* (Hua *et al.* 2005); (7) burrows (varied worms and slime moulds?), such as *Lamonte* (Meyer *et al.* 2014a); or (8) microfossils (mesomycetozoa), such as *Tianzhushania* (Huldtgren *et al.* 2011). With rare exceptions (Grazhdankin *et al.* 2012), the fossils listed above were aquatic, and probably marine. The Ediacaran Period predated the Cambrian explosion of animals and the Ordovician–Devonian adaptive radiation of plants (Erwin *et al.* 2011), but nevertheless was a time of unprecedented diversity on land and at sea (Retallack 2013a, 2014b, 2016a).

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No potential conflict of interest was reported by the author.

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