

RESEARCH ARTICLE

Damaged *Dickinsonia* specimens provide clues to Ediacaran vendobiont biology

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Abstract

Recently reported specimens of the enigmatic Ediacaran fossil *Dickinsonia* from Russia show damage and repair that provides evidence of how they grew, and of their biological affinities. Marginal and terminal areas of wilting deformation are necrotic zones separating regenerated growth, sometimes on two divergent axes, rather than a single axis. Necrotic zones of damage to *Dickinsonia* are not a thick scar or callus, like a wound or amputation. Nor are they smooth transitions to a regenerated tail or arm. The wilted necrotic zone is most like damage by freezing, salt, or sunburn of leaves and lichens, compatible with evidence of terrestrial habitat from associated frigid and gypsic paleosols. *Dickinsonia* did not regrow by postembryonic addition of modules from a subterminal or patterned growth zone as in earthworms, myriapods, trilobites, crustaceans, and lizards. Rather *Dickinsonia* post-embryonic regrowth from sublethal damage was from microscopic apical and lateral meristems, as in plants and lichens. Considered as fungal, *Dickinsonia*, and perhaps others of Class Vendobionta, were more likely Glomeromycota or Mucoromycotina, rather than Ascomycota or Basidiomycota.



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Introduction

Dickinsonia is an iconic Ediacaran fossil best known from South Australia [1–3], but also from central Australia [4], around the Russian White Sea [5], Russian Urals [6], Ukraine [7], India [8], and China [9]. It is a problematic fossil with interpretations ranging from lichen [10], xenophyophore foraminifer [11], soft coral [12], sea jelly [13], annelid worm [14], placozoan [15], or extinct non-bilateran eumetazoan [2]. *Dickinsonia* has been assigned to the problematic group Vendobionta, variously considered a kingdom [16], phylum [17], or class [4]. Recent reports of “intravital damage” [5] now allow reassessment of biological affinities and growth of *Dickinsonia*. The principal hypothesis tested here is whether *Dickinsonia* grew by tissue patterning, like animals, or by meristems, like plants, and pseudomeristems, like fungi. Growth hypotheses based on living organisms of these three kingdoms are compared with observed damaged zones, and post-damage regenerated portions of *Dickinsonia*.

Specimens recovered from sublethal damage during life test these hypotheses because regeneration from injury is distinct in different kingdoms of organisms [18]. Plants regenerate from apical or lateral meristems to one side of damage callus [19, 20], and fungi have similar

pseudomeristems [21, 22], but animals regenerate arms or tails from a blastema that does not leave a scar [23, 24]. Plants and fungi add modules from lateral meristems successively back from the apical meristem [19, 22], but animals add modules by cell patterning within subterminal growth zones [25–27]. Forms of damage are also distinct in the three kingdoms: swelling and scarring in animals [28–30], but browning, shrinkage, or wilting in plants [31–34] and fungi [21, 35, 36]. Wounded and regenerated Ediacaran fossils recently reported [5] can potentially reveal both biological affinities and mechanisms of growth of *Dickinsonia*.

Materials and methods

Dickinsonia menneri and *D. tenuis* fossils discussed here (Figs 1 and 2) are from the Ediacaran, Ust Pinega Formation at the Lyamtsa locality of the southeastern White Sea region of Russia, and are all repositied in the Paleontological Institute of Moscow [37, 38]. Of particular interest are specimens with unusual morphology interpreted as “intravital damage”, or non-fatal wounding that was later repaired [5, 39]. This paper is a redescription of the damage within the context of a non-genetic polarity terminology specific to *Dickinsonia* [40], based on excellent photographs and sketches provided by Andrey Ivantsov. It is a wide-ranging search among living organisms for anything morphologically comparable with the disrupted zone, and regrown addition. Implications of these comparisons are then considered within the context of other evidence on the biology and paleoenvironments of *Dickinsonia*.

Observations of damaged and recovered *Dickinsonia*

Hoekzema et al. [40] propose useful non-genetic terms for the distinctly different ends of *Dickinsonia*: deltoidal region for the end with a triangular flat region like the keystone of an arch, and antideltoidal region for the other end of invaginated modules (Fig 1A). This study is concerned with the antideltoidal region of specimens with extensive disrupted modules right across the fossil (Fig 2), especially “two-sided deformation” [5]. The disrupted zone is a highly deformed and wrinkled area between the main part of the fossil and an additional cordate or bilobed addition, here given the non-genetic name “antideltoidal tag”.

Transverse divisions of *Dickinsonia* have long been considered “segments” like those of annelids [14], but they rarely continue across the midline [1, 2, 41], where they are usually offset in zigzag fashion [16]. The term “module” suggested by Evans et al. [2] is preferred here, including mainly lateral modules. Whether deltoidal or antideltoidal modules can be considered basal or terminal modules, heads or holdfasts, is the central controversy addressed in this paper.

The interpretation of the disrupted zone by Ivantsov et al. [5] as “intravital damage” is accepted here as an assumption of this study, based on the continuation of the antideltoidal tag, or pair of tags. These specimens appear to be exceptional damage rather than regular or common growth interruptions, because very few specimens are known. Other specimens of *Dickinsonia* do not show recovery or repair of wrinkled or torn margins, but rather shredding to angular pieces, disruption by cracks extending into underlying sediment, stretching by sediment deformation, partial consumption by burrows or trails, excision of arcuate sections, or serial “footprints” from intermittent motion or transport [1–3, 8, 9, 42–45]. *Dickinsonia* did not necessarily move of its own accord, because the “footprints” may be “glacier mice”, or polsters frozen and driven by wind on melting ice [46]. These other fragments and deformed specimens reveal much about the tough integument and death of *Dickinsonia*, particularly a range of ductile to brittle behavior, interpreted here as degrees of freezing or desiccation of a normally pliable integument before burial.

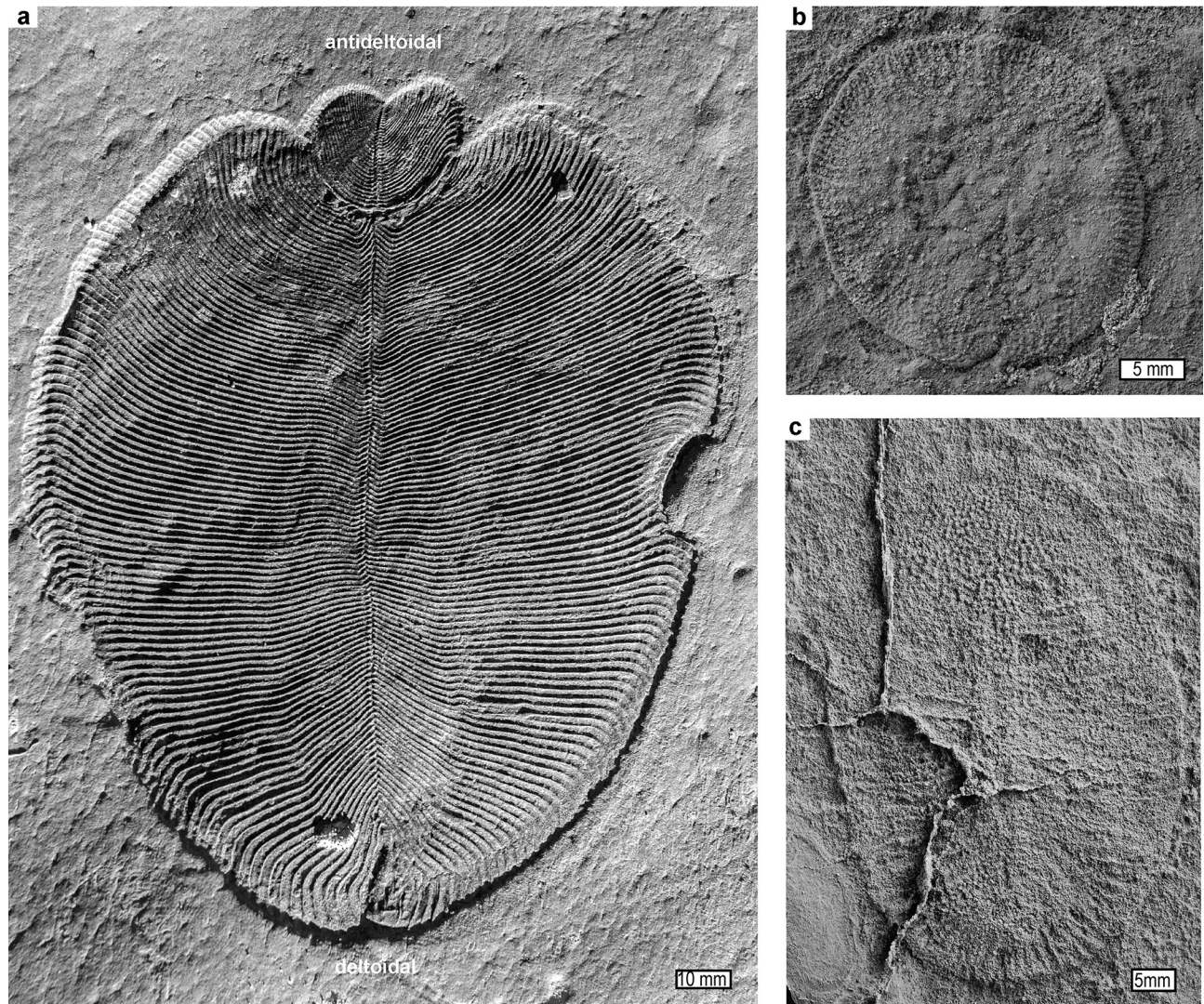


Fig 1. Fossil vendobionts from the Lyamtsa locality of Ediacaran, Ust Pinega Formation of the White Sea region: a, vendobiont *Dickinsonia menneri*; b, vendobiont *Yorgia waggoneri*; c, vendobiont *Dickinsonia tenuis*. Specimen numbers in the Paleontological Institute Moscow are PIN4716/5170 (a), PIN3993/5501 (b), PIN3993/850 (c), and images are courtesy of A. Ivantsov.

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The damaged Russian specimens are negative hyporeliefs on the soles of overlying slabs, as usual for *Dickinsonia*, and the disrupted wrinkled zone bulges to levels that would have been below the original upper surface. The bulges were depressions with flanking narrow ridges on the original body below the covering slab, and formed a zone of deformed shrinkage separating the antideltoidal tag, or tags. The bulges are wrinkled with high relief as if shrunken and desiccated, so differ fundamentally from Ediacaran non-resistant or sunken compressions of Wade [47], best known from *Nemiana* [48]. Burial compaction of *Nemiana* with jellylike consistence resulted in a convex hyporelief on the overlying slab, but *Dickinsonia* was far from jellylike as revealed by specimens lacerated into brittle shards [3, 45]. *Dickinsonia* fossils are concave hyporeliefs generally taken as evidence of a compaction-resistant biopolymer [47, 48]. The distinction between levels of the disrupted zone and the rest of *Dickinsonia* may reflect loss of compaction-resistance by pre-burial wilting, shrinkage, or hollowing out within that zone [42].

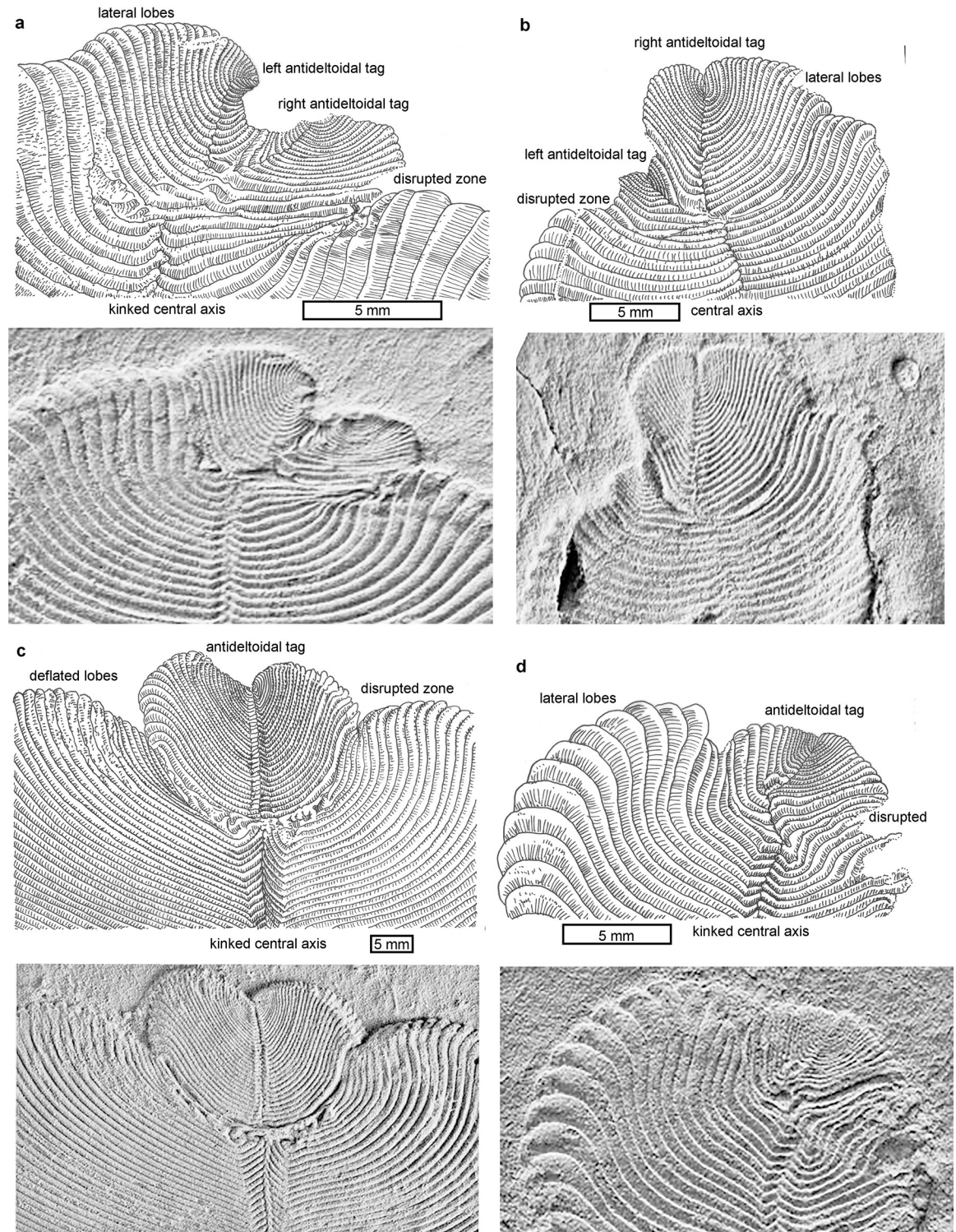


Fig 2. Recovery from damage to the antideltoidal end of *Dickinsonia menneri* from the Ediacaran, Ust Pinega Formation, at the Lyamtsa locality of the southeastern White Sea region Russia, using non-genetic terminology [40]. Fig 2C is the same specimen as Fig 1A. Specimens are PIN4176/5188 (a), PIN4176/5146 (b), PIN4176/5170 (c), PIN4176/5182 (d).

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In some cases, there is a single antideltoidal tag (Fig 2C and 2D), but in other cases there are two tags (Fig 2A and 2B). Paired tags diverge laterally, then curve parallel with the original axis toward the end. One of the antideltoidal tags originates laterally one module before the other tag, just as modules on the main body alternate along the midline.

Antideltoidal tags separated by a disrupted zone are the main puzzle addressed by this paper, but also notable is a kinked central axis in three of the four specimens illustrated in Fig 2, as if lesser damage preceded the more extensively disrupted zone. Similar shrinkage and buckling is also seen in other marginal areas of this Russian collection of *Dickinsonia* [5]. Another anomalous feature in these Russian *Dickinsonia* (Fig 1C) and the similar genus *Yorgia* (Fig 1B) is a pustulose texture of spherical bodies within an upper integument [38].

Interpretation of *Dickinsonia* disrupted zone

Infection

Infection of animals and plants by pathogens and parasites usually includes swelling into blisters or galls preserved in fossil leaves, shells and bones [49]. These swellings in soft-bodied organisms are thick callus or scar tissue [28, 29, 50]. The pustulose texture of the upper surface of some *Dickinsonia* (Fig 1B and 1C) may be infection comparable with tar spot fungus, *Rhytisma acerinum*; [51]. However other explanations are also plausible, for example, as a tubercular ornament [39], or as reproductive structures [10]. Infection is not a good explanation for the observed withered and shrunken, disrupted zone of *Dickinsonia*, because the disrupted zone is neither pustulose, swollen, nor hollow (Figs 1 and 2). Furthermore, the whole organism would not have been infected, because isomers before and after the disruption are unaffected.

Atavism

Atavisms are genetic mistakes that recapitulate evolutionary history, such as tails in humans [52], extra digits in horse feet [53], or multiheaded cnidarian polyps [54]. Could antideltoidal tags in late Ediacaran *Dickinsonia* be rare outgrowths of lobes recapitulating multilobed middle Ediacaran vendobionts? No atavisms have previously been noted in Ediacaran fossils, but a plausible case is *Hylaecullulus fordi*, which has a complex branching system of fronds? Unlike the *Dickinsonia* specimens discussed here (Figs 1 and 2), adventitious fronds of *Hylaecullulus*, are not separated by a disrupted zone, and are part of a coherent fractal branch system [55]. The relationship of *Hylaecullulus* and other rangeomorphs to *Dickinsonia* is uncertain [56]. Disrupted zones of weakness separating supernumerary elements are not seen in growths that could be considered atavisms in modern or ancient examples [52–54]. The post-damage antideltoidal tags of *Dickinsonia* have disrupted zones distinct from atavisms.

Laceration scar or callus

Laceration of animals creates scars [57], and in plants it creates callus or resin [32, 49]. Injury to hard tissue such as teeth or shells also produces swelling and deformation of symmetry [29, 49]. Predation damage is unlikely for *Dickinsonia* given variable expression of deformation and lack of known large predators in the Ediacaran [5]. Comparable deformation is lacking in *Dickinsonia* consumed along worm trails [43]. In sponges, severe dismemberment to small fragments is repaired without scars or deformed zones [58, 59]. Scarless repair of injury is also found in placozoans, planarian worms, comb jellies, and cnidarian polyps [18, 60, 61], again unlike *Dickinsonia*. Scarless whole-body regeneration is not found in vertebrates [62], and scarless limb regeneration is lost in frogs after metamorphosis [24]. Recovery by scar and callus formation is mainly found in large perennial organisms [32, 49, 57], and *Dickinsonia* was both

large and perennial compared with associated fossils [63]. Scar and callus tissues form compact protruding seals, unlike the withered, disrupted zone of *Dickinsonia*, or the clean edges of dismembered *Dickinsonia* [2, 44, 45].

Frost, sunburn or salt injury

These three distinctly different causes of injury create similar effects in fungi and plants, distinct from their effects in animals. In humans, frostbite produces swelling, and then death of tissue, best treated by amputation or scraping back to live tissue, that then is a scar [28]. Damage of humans by salt and sunburn also causes swelling, blisters, peeling skin, and can result in scars [64], which also are unlike the disrupted zone of *Dickinsonia*. Freezing, hypersalinity, and sunburn do not create local disrupted growth zones in aquatic creatures, such as sea jellies or polychaetes, but kill, desiccate, and wither the whole organism [65, 66]. Frost, sunburn and salt injury of lichens results in death of the photosynthetic layer on thallus margins, and shrinking and death of the growth apex down to the hypothallus [35, 36]. The apex is then replaced by one or more lateral meristems to form an apical tag or tags elaborated from apical threads beyond the wilted and necrotic zone (Fig 3A and 3B), broadly similar to those observed in *Dickinsonia* (Fig 2). There has been controversy for *Dickinsonia* in interpreting a rim around the fossils as a hypothallus with branching hyphae [42], as scrape impressions in the sediment of the margin of a shrunken individual [14], as signs of self-propelled incipient motion [45], or as incipient dislodgement by basal freezing [46]. In plant leaves, frost, sunburn and salt injury shrink both palisade and mesenchyme cells of the margin. With loss of chloroplasts and chromophores, this results in browning, thinning, curling, and wrinkling [31–34, 67, 68].

Of the four alternatives considered here, sunburned and salt damaged leaves and lichens are the best modern analogy for the terminal disrupted zone of *Dickinsonia*. Unlike animal repair, there was only minor deformation anticipating the break-line, rather than distributed deformation, axial more than peripheral addition, and failure to completely restore the overall shape. By this analogy, antideltoidal ends of *Dickinsonia* were growth zones, and deltoidal ends were holdfasts or growth initials.

Interpretation of *Dickinsonia* antideltoidal tag

Budding

A common form of asexual reproduction in animals is budding, well known in living placozoans [69], sponges [70, 71], and cnidarians [72]. Budding also is preserved in fossil invertebrates [49, 73, 74]. Budding starts as an outgrowth from a stolon or other narrow part of the parent, then grows into another undeformed individual attached by an undisrupted narrow stalk. The newly budded individual is a replica of the parent, not a continuation of modified modules of the adult, as in the antideltoidal tags described here (Fig 2). Stolons are often long, but even short stolons have a constriction that allows the bud to detach from the parent, unlike the antideltoidal tag nestled within the end of *Dickinsonia* (Fig 2).

Limb regeneration

Limb and tail regeneration is well known in starfish [23] and amphibians [24], but regeneration also is known from 18 additional animal phyla [62]. Up to six tails can be regenerated by lizards, in an unusual branching structure [75]. Scar-less regenerated limbs are also recorded among fossil lizards and decapods, and are especially obvious when still smaller than the original limbs and tails [49]. Sponges regenerate entire colonies from small pieces with no evident

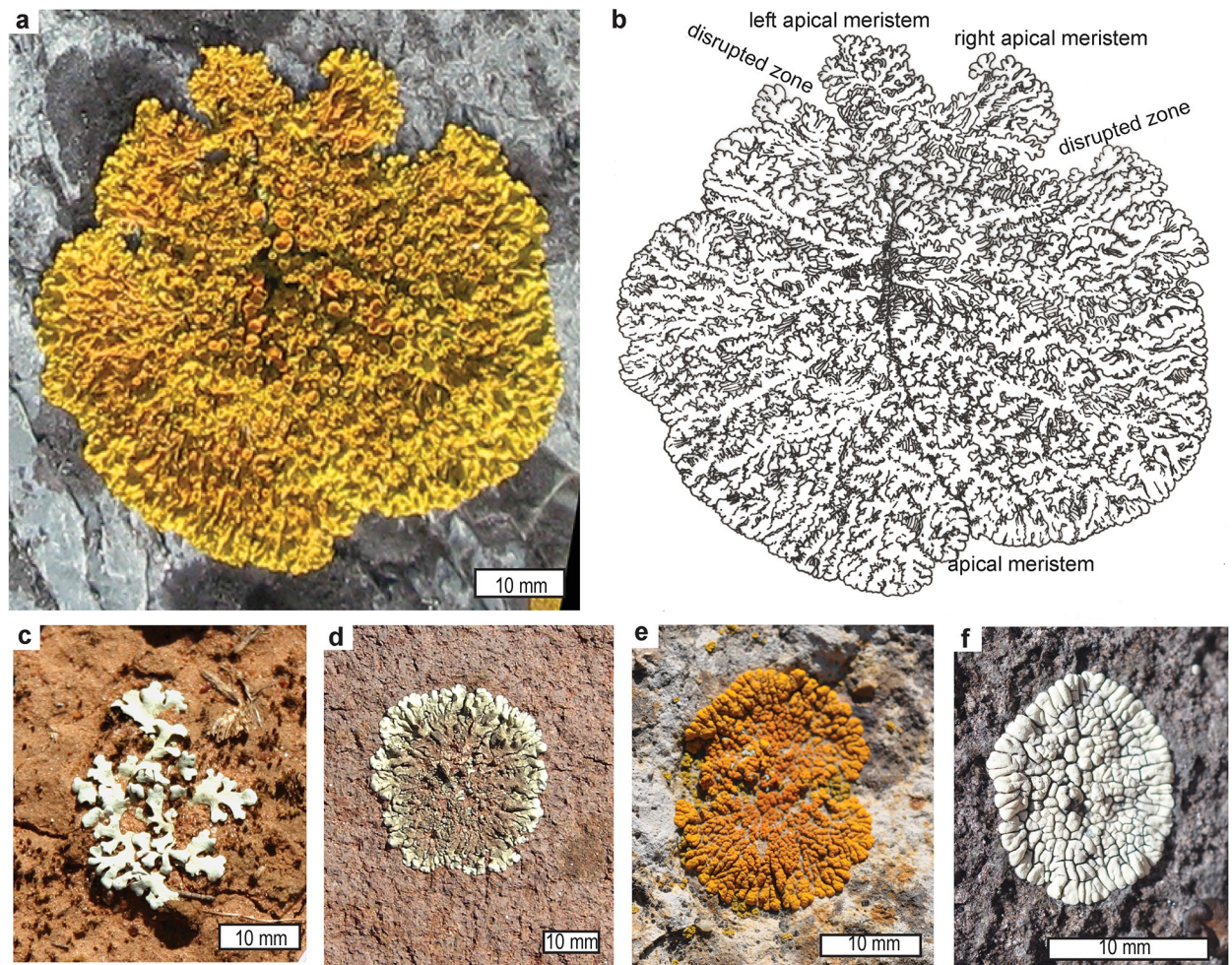


Fig 3. Modern lichens showing apical and lateral meristematic mode of growth: *Caloplaca verruculifera* image (a), and interpretive sketch of lobe disposition with apothecia removed (b), from rock platform exposure of Ediacaran, Gaskiers Formation, 4 m above sea level, St Marys, Newfoundland; lichen *Xanthoparmelia terrestris* on red soil between belah (*Casuarina cristata*) trees at Back Creek State Forest 16 km east of West Wyalong, N.S.W., Australia (c), *Xanthoparmelia plittsi* (d) and *Polycauliona ignea* (e) on welded tuff of Oligocene, John Day Formation on Carroll Rim, Painted Hills State Park, Oregon, and *Dimelaena oreina* (f) on Steens Basalt at Paisley Caves, Oregon.

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scarring or damaged zones [58, 59], and so can placozoans, planarian worms, comb jellies, cnidarian polyps and molluscs [18, 60–62, 76]. Scar-free regeneration of limbs is achieved through many processes, including immune system removal of damage, cell dedifferentiation, cell transdifferentiation, and cell patterning in a broad blastema, rather than from a narrow meristem [18, 24]. Lack of a disrupted zone in regenerated animal parts is distinct from the antideltoidal tag defined by a disrupted zone in *Dickinsonia* (Figs 1 and 2).

Subterminal growth zone

In animals, body parts are specified by cell patterning in the developing embryo, including terminal growth of tails [41, 77]. Postembryonic terminal regeneration of vertebrate tails is also achieved by cell patterning in cartilage of the elongating blastema cone, rather than terminal or intercalary addition of ossified vertebrae [78]. An animal model of interstitial regeneration of *Dickinsonia* advocated by Ivantsov et al. [5] would have resulted in seamless tail regrowth [75], unlike the fossils discussed here. Segments also are added during postembryonic growth

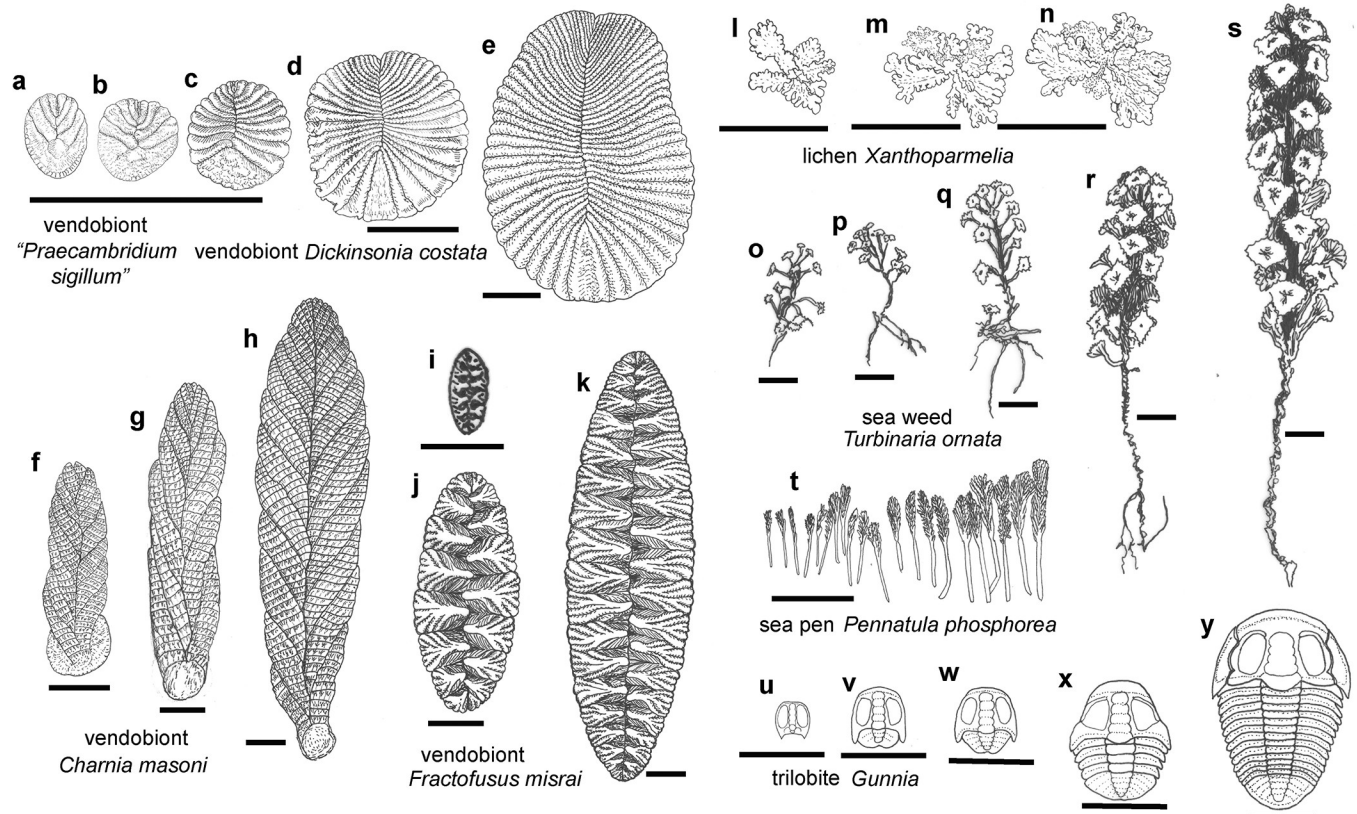


Fig 4. Growth series of vendobionts (a-k), living organisms (i-t), and trilobite (u-y): a-b, “*Praecambridium sigillum*” from the Ediacara Member of the Rawnsley Quartzite Ediacara Hills, South Australia [94]; c-e, *Dickinsonia costata* from the Ediacara Member of the Rawnsley Quartzite Ediacara Hills, South Australia [14, 96]; f-h, *Charnia masoni* [55, 86] from the Drook Formation at Drook Newfoundland (f), Mistaken Point Formation at Mistaken Point, Newfoundland (g), and Bradgate Formation in Charnwood Forest, England (h); i-k, *Fractofusus misrai* from the Mistaken Point Formation at Mistaken Point, Newfoundland [114, 146]; l-n, crustose lichen *Xanthoparmelia* sp. indet. on a granite tombstone, in successive years 8 Nov. 2005, 27 Sept 2006 and 21 May 2007, Petersham, Massachusetts [81]; o-s, phaeophyte alga *Turbinaria ornata* from Moorea, French Polynesia [88]; t, sea pen *Pennatula phosphorea* from the North Sea, UK [26]; u-y, trilobite *Gunnia* sp. indet. from the Middle Cambrian, Gaotai Formation, from Balang, Guizhou Province, China [27]. Scale bars all 10 mm.

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from a subterminal growth zone in sea pens [26], trilobites [27], millipedes [79], and earthworms [25]. The growth zone is subterminal in animals, because the terminal segment is established by embryonic cell patterning count-down early after the head. That terminal segment is variously known as pygidium in trilobites [27], and periproct in millipedes [79], and earthworms [25]. The pygidium and periproct are at least millimetric in size, and would have been preserved in *Dickinsonia* with fine-grained clayey matrix like the Russian specimens. They have never been found, and the antideltoidal meristem was evidently microscopic. The antideltoidal tags in *Dickinsonia* are at the end and separated from the rest of the body by the disrupted zone, unlike subterminal growth zones in animals (Figs 4 and 5).

Apical and lateral meristems

A system of apical and lateral pseudomeristems is found in fungi [21, 22, 80, 81] and a system of meristems in plants [19, 20]. Pseudomeristems and pseudoparenchyma of lichens mature to appear very similar to meristems and parenchyma, but form by septation of hyphae rather than proliferation of cubic cells [82]. The apical meristem is the terminus of the main shoot, but lateral meristems are the tips of branches. These laterals may emerge as leaders when the

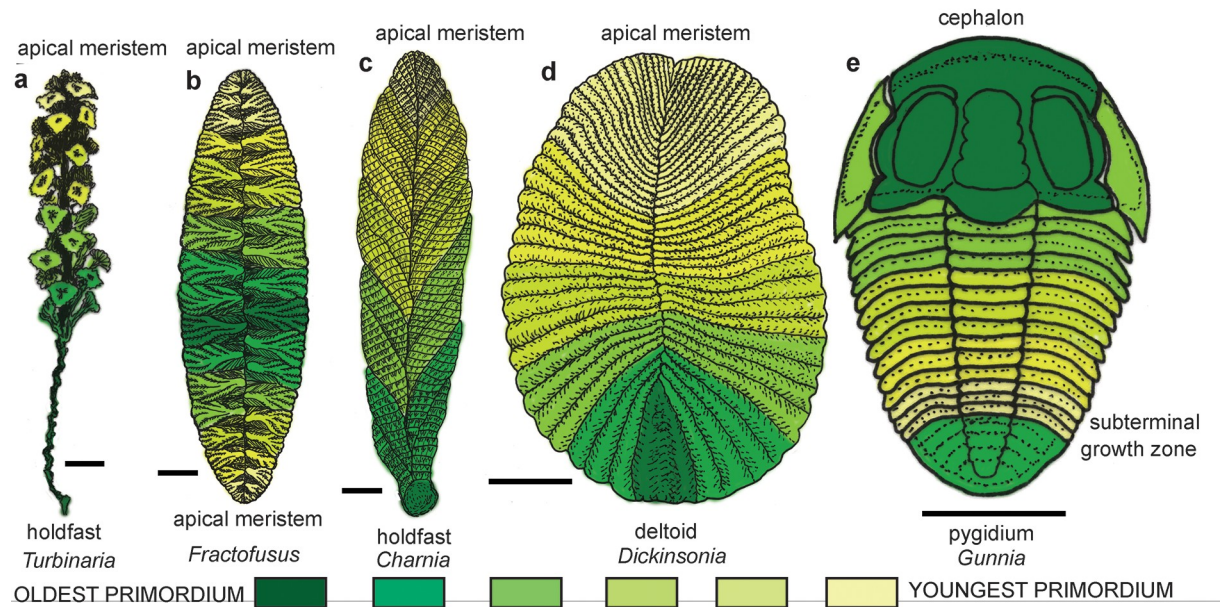


Fig 5. Interpreted relative age of mature examples of vendobionts, sea weeds, sea pens and trilobite based on Fig 3: a, phaeophyte alga *Turbinaria ornata* from Moorea, French Polynesia [88]; b, vendobiont *Fractofusus misrai* from the Mistaken Point Formation at Mistaken Point, Newfoundland [114]; c, vendobiont *Charnia masoni* from Bradgate Formation at Charnwood Forest, England [86]; d, vendobiont *Dickinsonia costata* from the Ediacara Member of the Rawnsley Quartzite Ediacara Hills, South Australia [14]; e, trilobite *Gunnia* sp. indet. from the Middle Cambrian, Gaotai Formation, from Balang, Guizhou Province, China [27]. Scale bars all 10 mm.

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apical meristem is lethally damaged [19, 83]. Growth on two opposed apical pseudomeristems and numerous radial laterals explains the growth of lichens (Fig 3), and the Ediacaran fossil *Fractofusus* (Fig 4), and such opposed meristems are known in non-vascular plants [84, 85]. The growth pattern of other Ediacaran fossils, such as *Charnia* [26, 86, 87], show a holdfast at the base, and an apical meristem at the other end (Fig 4), most like algae such as *Turbinaria* [88]. Growth from the anti-holdfast end is also noted by Dunn et al. [89], who also propose, without justification, continuing growth in the stalk. By the contrasting rangeomorph model of Antcliffe and Brasier [26], the deltoidal region of *Dickinsonia* is a holdfast rather than a head, and the antideltoidal region is an apical meristem or pseudomeristem. The deltoid holdfast interpretation is especially suggested by the rounded terminal module of “*Praecambridium sigillum*” (Fig 4), proposed as juveniles of *Dickinsonia* by Runnegar [14]. Twin antideltoidal tags can thus be explained as axial lateral meristems emerging after damage of the apical meristem. The two antideltoidals alternate like all the lateral modules of the zigzag central suture representing alternate fractal growth. Comparable leaders are created by removal of the terminal meristem during pollarding of trees [83].

Growth of *Dickinsonia*

Dickinsonia grew with addition of modules (Fig 4), but different growth alternatives have been proposed. Is the deltoidal end a head or a holdfast? Is the deltoidal end anterior or posterior? Hoekzema et al. [40] plotted both antideltoidal-first and deltoidal-first growth models and found changing rates of module length through life to maintain an ovoid overall shape. The deltoidal-first pattern is a less extreme change in relative module length, so they interpreted the deltoidal as the oldest part, thus literally anterior, and the antideltoidal part as the youngest part, thus literally posterior. Another meaning of anterior is the direction of movement, such as head-first in vertebrates, but direction of movement is unclear in serial imprints of

Dickinsonia [2], misinterpreted as trails [46, 90]. Hoekzema et al. [40] rejected the antideltoidal-first hypothesis because that “trend in our studied specimens is not unidirectional (as would be expected in an organism with a well-regulated growth programme).” Hoekzema et al. [40] also assumed that it was an animal which grew by subterminal addition, so that the deltoidal would be the terminal posterior module comparable with a periproct or pygidium of trilobites (Fig 4). Dunn et al. [89] mark both the deltoidal and antideltoidal as the oldest parts (both anterior? or unresolved?), with modules interpolated between. Dunn et al. [89] also align the antideltoidal with an insect head (anterior) and deltoidal with an insect tail (posterior). By both interpretations, *Dickinsonia* was an animal up to 1.4 m long [42] with a microscopic head: a head too small to be observed in any known fossil impression. Growth from the deltoidal end, or subterminal to it, is falsified by antideltoidal but not deltoidal regrowth, represented by antideltoidal tags [5, 45].

Another view of Runnegar [14], followed by others [5, 41, 91–93], regards the deltoidal as an anterior “head”, and the antideltoidal as a posterior “tail” most like those of annelids and insects, rather than postanal tails of lizards and other vertebrates. Runnegar [14] supported this interpretation by adding “*Praecambridium sigillum*” [94], with its disc on one end, as a juvenile to a growth series of *Dickinsonia* (Fig 3). Others [95] have also argued that *Dickinsonia* fossils with proportionally widest deltoids were youngest. This interpretation is a holdover from an earlier view of *Dickinsonia* as an annelid, including interpretation of the midline as a gut connecting a deltoidal mouth and antideltoidal anus [14, 96]. My own examination of hundreds of specimens has been unable to identify digestive anatomy [42], and there is widespread agreement that *Dickinsonia* lacked digestive tract, mouth, anus, or periproct [15, 44, 93]. Elongation of the antideltoidal end in progressively older specimens is supported by both growth series [14, 42] and antideltoidal tags [5, 45]. Nor do series of impressions reveal that *Dickinsonia* moved of its own accord in the direction of the deltoidal region [2], because that older region would have been more heavily frozen and driven by wind after basal melting [46].

A third view of Retallack [10, 42, 48] regards the deltoidal as an anterior holdfast, supporting an antideltoidal posterior axis, as in Ediacaran fronds such as *Charnia* (Figs 4F–4H). The deltoid may have originally been circular and the full width of the body (14), but the deltoid diminished in relative width with addition of terminal modules (Figs 4A–4E). This deltoid-holdfast interpretation explains antideltoidal tags and disrupted zones as sublethal interruption of terminal growth (Fig 2). Antideltoidal regeneration can be explained as due to a system of apical and lateral meristems as documented in lichens [21, 22, 81] and plants [19, 20, 97]. Paired antideltoidal tags may be lateral meristems resuming growth after damage of posterior modules and death of the terminal meristem. *Dickinsonia* rarely shows true segmentation of creases right across the body [41, 93], but commonly had a glide symmetry of modules alternating along a midline [16, 98], including divergent paired antideltoidal tags (Fig 2A and 2B). Wade [96] argued for a small antideltoidal terminal module of *Dickinsonia* like the periproct of polychaetes, which she considered modern descendants of *Dickinsonia*. No such terminal module has been demonstrated [40, 89]. The generative point of the antideltoidal end was microscopic and flanked by small, thin, modules, like an apical meristem flanked by young, developing, podetia or leaves of fungi and plants [19, 22].

The developmental implications of suggested placozoan affinities for *Dickinsonia* [15] are unclear, because living placozoans such as *Trichoplax* lack segmentation and anterior-posterior differentiation (Fig 6A). *Trichoplax* does have dorso-ventral differentiation, only 4 cell types, and a single HOX gene [60, 99]. *Trichoplax* alternates between spherical and flattened bodies formed by radial cell-division, and can divide into two halves separated by a thread or stolon [60, 69, 100], which is eventually severed (Fig 6B–6D). This unique growth form may be relevant to a placozoan interpretation of *Dickinsonia* if placozoans represent an evolutionary

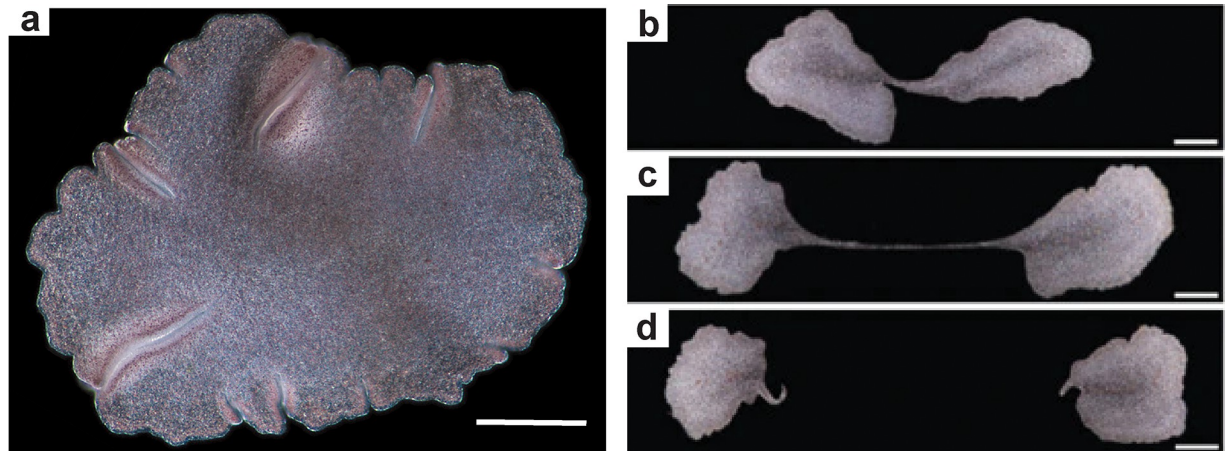


Fig 6. The placozoan *Trichoplax adhaerens* (a), and its reproduction by fission (b-d). Scales in panels a-d are 200 μ m. From [60] with permission.

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transition from fungi to metazoans [99, 100], because then apical and lateral meristematic growth of fungi and plants would have been lost before evolution of subterminal addition in animals [25, 27, 79]. However, the idea of placozoans as the earliest diverging animal lineage is now doubtful, with animal derivation from unicellular choanoflagellates more likely [101, 102].

More cogent evidence for the distinctly different development of plants, fungi, and animals is phylogenomic. The topology of molecular trees has varied greatly over the years, but many agree that plants, fungi, and animals developed multicellularity independently from unicellular ancestors [103–105]. The three kingdoms also have different genes for development: KNOX and MADS for plant meristematic growth, MADS for fungal and lichen pseudomeristematic growth, and HOX for animal cell patterning [99, 106–108]. A less compelling generalization, because of exceptions such as metamorphosis and long-lived animals, is that animal development is mainly embryonic, and plant-fungus development is mainly postembryonic [109]. This generalization is reflected in the generalization of determinate growth for animals, but indeterminate growth for plants and fungi. Elephants, alligators and sea turtles have been considered an exception to this generalization, but comprehensive studies have demonstrated that all three are determinate, with a distinct age of no further growth [110–112]. Nevertheless, animals such as placozoans and planarian worms may have indeterminate growth [113]. Indeterminate growth has been demonstrated for *Dickinsonia* [42].

The scheme of development for *Dickinsonia* preferred here is outlined in Fig 5, in which darkest hues are oldest and anterior, and the lightest hues are youngest and posterior in terms of the branch order of their module primordia. Each module has a lateral meristem which is likely a diffuse marginal meristem like that of developing leaf, rather than a separate shoot [83]. In a meristematic system, Ediacaran *Fractofusus* (Fig 5B) [114] had divergent apical meristems like the development of lichens (Fig 3), but Ediacaran *Charnia* (Fig 5C) [26] had a single apical meristem, like brown algae (Fig 5A) [88], and lichens such as *Cladonia* [22]. So the question is whether *Dickinsonia* added modules from a terminal meristem like an alga or fungus, or in a subterminal growth zone like a trilobite (Fig 5E)? Antideltoidal tags and multiple regenerative axes are evidence that *Dickinsonia* had a meristematic system like a plant or fungus. Preservation of a disrupted zone between normally formed parts of large specimens [5] also implies temporary interruption of indeterminate growth of a perennial structure, rather than

injury of a short-lived creature with limited determinate growth. *Dickinsonia* did not grow and regenerate like arthropods or annelids, nor like sponges or placozoans.

Other evidence for biology of *Dickinsonia*

Sedimentary context

Dickinsonia in South Australia has been interpreted as a shallow marine or intertidal creature, thrown up by storms onto the shore [115, 116], but revised facies analysis interpreted them as entirely submarine [117]. Comparable facies analysis of Russian *Dickinsonia* found them in middle to upper shoreface prodelta facies [118]. Doubts about marine habitats came from the discovery in South Australia of *Dickinsonia* atop paleosols, showing soil textures, carbonate nodules with pedogenic stable isotopic covariance, desert rose pseudomorphs, periglacial convolutions, and hydrolytic chemical weathering profiles [48, 63, 119]. Paleosols directly below *Dickinsonia* have also been found in central Australia [120], India [6], and Russia [8, 90]. Drab-haloed threads down into red paleosols below *Dickinsonia* [6, 63] are *Prasinema*: traces of mycelia or rope-forming cyanobacteria common in paleosols [121–123]. These subvertical drab threads disturb bedding and create massive red beds in the field and in thin sections [48], unlike the laminated microbial mat interpretation of the same beds [2, 124]. Ediacaran “Mattressland” vendobionts of red beds [120] may be contrasted with Ediacaran grey stromatolitic carbonates and shaley turbidites with marine tubular fossils such as *Gaojianshanina*, *Conotubus*, *Cloudina*, and *Namacalathus* of Ediacaran “Wormworld” [125–127].

Ediacaran paleosols include periglacial convolutions and ground ice as evidence for freezing [48, 90, 128], here proposed as a plausible explanation for disrupted zones of *Dickinsonia*. Gypsum desert roses in the paleosols [63, 116, 119] support the idea of salt stress as a cause for disrupted zones of *Dickinsonia*. Also evidence for land exposure of *Dickinsonia* are recent reports [129, 130] of eolian sedimentary structures: setulfs (obstacle accumulations), wind dissected ripples (transverse scour), climbing translational stratification (adhesion ripples), and interflag sandstone laminae.

Trace elements

Analysis of *Dickinsonia* from central and South Australia, and Russian White Sea and Urals show only traces of boron, much lower than in marine rocks. After adjustment for burial alteration and comparison with genuine marine deposits from the same regions, this is evidence that *Dickinsonia* was non-marine [127]. Very early diagenetic cements predating burial compaction of Ediacaran holdfasts in sandstones [131], have Ge/Si ratios >1 $\mu\text{mol/mol}$ characteristic of soil, not aquatic sediment or cements [132]. Dating by $^{234}\text{U}/^{238}\text{U}$ of iron oxides on Ediacaran fossil cover slabs [133] are an inadequate test for recent versus Ediacaran oxidation because the half-life of that rarely used isotopic system, could not reveal Ediacaran age minerals if they were there. There is also evidence for pervasive Ediacaran oxidation of red beds from alternating red and green beds, from claystone breccias with both red and green clasts, from red beds deep in boreholes below green and gray beds, and from tau analysis of ferric and ferrous iron within beds [63, 119, 129, 134].

Trace fossils

Sequential imprints have been interpreted as trails of motile *Dickinsonia* [2, 135, 136], but are more likely sessile individuals displaced by periglacial frost boils [46, 90], or impressions of “vagrant lichens” or “snow mice” moved intermittently by gusts of wind on ground ice [137–139]. Elongate marks a quarter of the width of the *Dickinsonia* have also been interpreted as

trails of movement [45, 140], but that interpretation is precluded by their width disparity. Arcuate marginal lacerations and overfolds are not necessarily evidence of current liftoff [1], but evidence that *Dickinsonia* was attached to the substrate by forces greater than needed to tear the body apart [141]. The nature of *Dickinsonia* attachment to the substrate is revealed by thin sections showing a thick upper pellicle above chambers, but ragged lower boundary with tubular structures down into the matrix [48]. Narrow animal trails consuming *Dickinsonia* were considered scavenging of buried dead bodies [43], but those *Dickinsonia* modules are undecayed and the trails have lateral levees unlike subsurface burrows [142]. *Dickinsonia* shows neither avoidance nor scar-reaction to the attack, which was more likely a case of surface herbivory. Assemblages with *Dickinsonia* and other vendobionts also show complex rank abundance distribution [143], high β -diversity [144], low interspecific interactions [145], and vegetative propagation [146], unlike modern to Ediacaran or Phanerozoic fossil marine benthic communities [125, 126], and more like terrestrial vegetation [144, 145]. Vendobionts interacted, reproduced, and evolved more like plants and lichens, than like animals.

Taphonomy

Preservation of *Dickinsonia* and other vendobionts is problematic because they show higher relief than soft-bodied animal fossils, and are preserved more like plants or fungi with burial-compaction-resistant biopolymers such as cellulose, or chitin [3, 10, 42]. The idea of rheological fill beneath a rigid carapace [44] is falsified by lack of internal soft-sediment deformation upwards into the carapace. Instead, thin sections reveal that orthogonal, chambered structure and matrix to filaments below were already partly filled with substrate grains and lacked lamination or other traces of microbial mats [44, 48]. Alternatively, relief may have been supported by early diagenetic pyritization [147], or silicification [131].

Biomarkers

The sponge biomarker 24-isopropylcholesterane is common in indisputably marine Ediacaran rocks of Oman and China, but missing in shales with *Dickinsonia* in Russia [148, 149]. Also in contrast with known Ediacaran marine rocks, Russian shales have (1) unusually high and variable ratio of hopanes/steranes (1.6 to 119, thus variable but generally more bacteria than algae), (2) high and variable $\delta^{15}\text{N}$ (-2.8 ‰ outlier, mostly +3.5 to +6.5 ‰, thus generally without nitrate limitation); (3) high and variable $\delta^{13}\text{C}_{\text{org}}$ (-23.0 to -33.1 ‰, thus cyanobacterial or algal photosynthetic carbon-concentration mechanisms), and (4) low total organic carbon (0.09 to 1.06 wt %, thus highly oxidized). These biomarker levels [from 148, 149] thus support evidence of low boron content [127, 150], that European Vendian shales were deposited in and around lakes or coastal lagoons rather than in the open ocean.

Cholestanes (C27) in *Dickinsonia* [151] are found in animals, but also in fungi and red algae [149]. Cholesterol (C27) is the main sterol in red algae [152, 153]. Glomeromycotan fungi also produce comparable C27 cholesterol [154] and are represented in Ediacaran fossil assemblages by acritarchs [155] and permineralized fragments [156, 157]. Up to 15% cholesterol (C27), along with up to 85% 24-ethyl cholesterol (C29), is present in 5 species of modern symbiotic mycorrhizal *Glomus* (Glomeromycota) [158]. Saprophytic and parasitic fungi with 78–100% cholesterol include *Pneumocystis* (Ascomycota) [159], *Conidiolobus* (Zygomycota) [160], *Blastocladiella*, *Allomyces* (both Blastocladiomycota) [160], *Rhizophlyctis*, *Monoblepharella* and *Chytridium* (all Chytridiomycota) [161]. This phylogenetic distribution suggests that cholesterol is basal to fungi, and ergosterol (C28) evolved later [160], perhaps before Ediacaran by 650 Ma [153]. Fungal affinities for *Dickinsonia* may explain the declining ratios of stigmasterane/cholestane in progressively larger and older specimens [151–Fig 1D and 1E]. This would

not be such a regular pattern if an animal were fouled in old age by green algae with stigmasterol (C29), or if smaller specimens were more affected by local diffusion of algal steroids than larger specimens during burial, but observed regularity is compatible with long-term fungal growth from controlled green algal symbionts with stigmasterol [162]. The balance of steroids, especially lack of C30 steranes in *Dickinsonia* [151], also falsify interpretation as xenophyophore foraminifera [11]. Modern contamination is a concern with the available steroid analyses of Russian *Dickinsonia* [151], considering low amounts of total organic carbon, and weathering of local outcrops, [149]. The virtually unracemized 5 β (H) stereochemistry of bacterially-degraded cholesterol (coprostanol), known mainly from animal digestive tracts and sewage [163], is further support for contamination by modern animal feces [149].

Biological affinities of *Dickinsonia*

Damaged *Dickinsonia* described here rule out animal affinities for *Dickinsonia*, but not algal or fungal affinities. Ford [164] was first to propose algal affinities for *Charnia*. Other fossils from Charnwood Forest, England, and Mistaken Point, Newfoundland, also have the general appearance and meristematic growth system of algal fronds [26, 55, 86]. Meristematic growth of *Charnia* has been disputed [89], as well as its inclusion with vendobionts [56]. Evidence from steranes of *Dickinsonia* [151] restrict the likely algal group to Rhodophyta [152, 153]. Algal interpretations for vendobionts are unpopular for a variety of reasons: lack of branching bases like algal rhizomorphs, strong relief of the fossils requiring stronger biopolymers than cellulose in algae, lack of mineralization, load-bearing stalks of rangeomorphs tapering upward in a way unable to flex with currents, large internal chambers, within-substrate habit of erniettomorphs, and substrate-hugging habit of dickinsoniamorphs [10, 16, 42, 48].

Similarities of vendobionts with crustose lichens [10] have also are unpopular [2, 151], in part because of different concepts of lichens. A lichen is defined as fungi with symbiotic algae or cyanobacteria, but recent redefinition of lichens as dikaryan fungi only (Ascomycota and Basidiomycota), means that lichens could not be older than Silurian, given palynological lack of evidence for Dikarya before then [165]. Dikaryan lichens have photobionts immobilized by haustorial connections (ectolichens), but lichenized glomeromycotan fungi such as *Geosiphon* engulf the photobionts within a vesicle (endolichens). These differences are comparable with endomycorrhizae and ectomycorrhizae in relationship to their plant hosts [166]. A case has also been made that *Geosiphon* should not be considered a lichen [167], in another attempt to restrict the commonly used term lichen to particular fungal clades and constructions.

Geosiphon is a glomeromycotan endolichen with cyanobacterial symbionts enclosed within an interior vesicle [168], similar to 2.1 Ga *Diskagma* (Fig 7C–7F) [169]. Other fossil evidence for glomeromycotan or mucoromycotinan fungi comes from spores as old as 1.5 Ga [155, 170], and permineralized lichens as old as 0.64 Ga [156, 157]. *Geosiphon* and *Diskagma* are plausible glomeromycotan endolichen models for *Dickinsonia* if the internal chambers of *Dickinsonia* (Fig 7A and 7B), housed photosymbionts. Unlike *Geosiphon* however, the photobionts of *Dickinsonia* would have been chlorophyte algae rather than cyanobacteria, judging from sterane biomarkers in *Dickinsonia* [151].

Another plausible models for *Dickinsonia* as an ectolichen are extinct nematophytes, such as *Prototaxites* (Fig 7H and 7I), which had coccoid chlorophyte photobionts with haustorial connections within cortical nests of loose inward-curling hyphae [85, 171]. Similar haustorial connections to coccoid photobionts have also been found in an unnamed early Ediacaran fungus from China [157]. The mainly aseptate hyphae of *Prototaxites* have been interpreted as evidence of glomeromycotan or mucoromycotinan affinities [85, 171]. *Prototaxites* has also been interpreted as an ascomycotan fungus, complete with hymenium [172], which does not appear

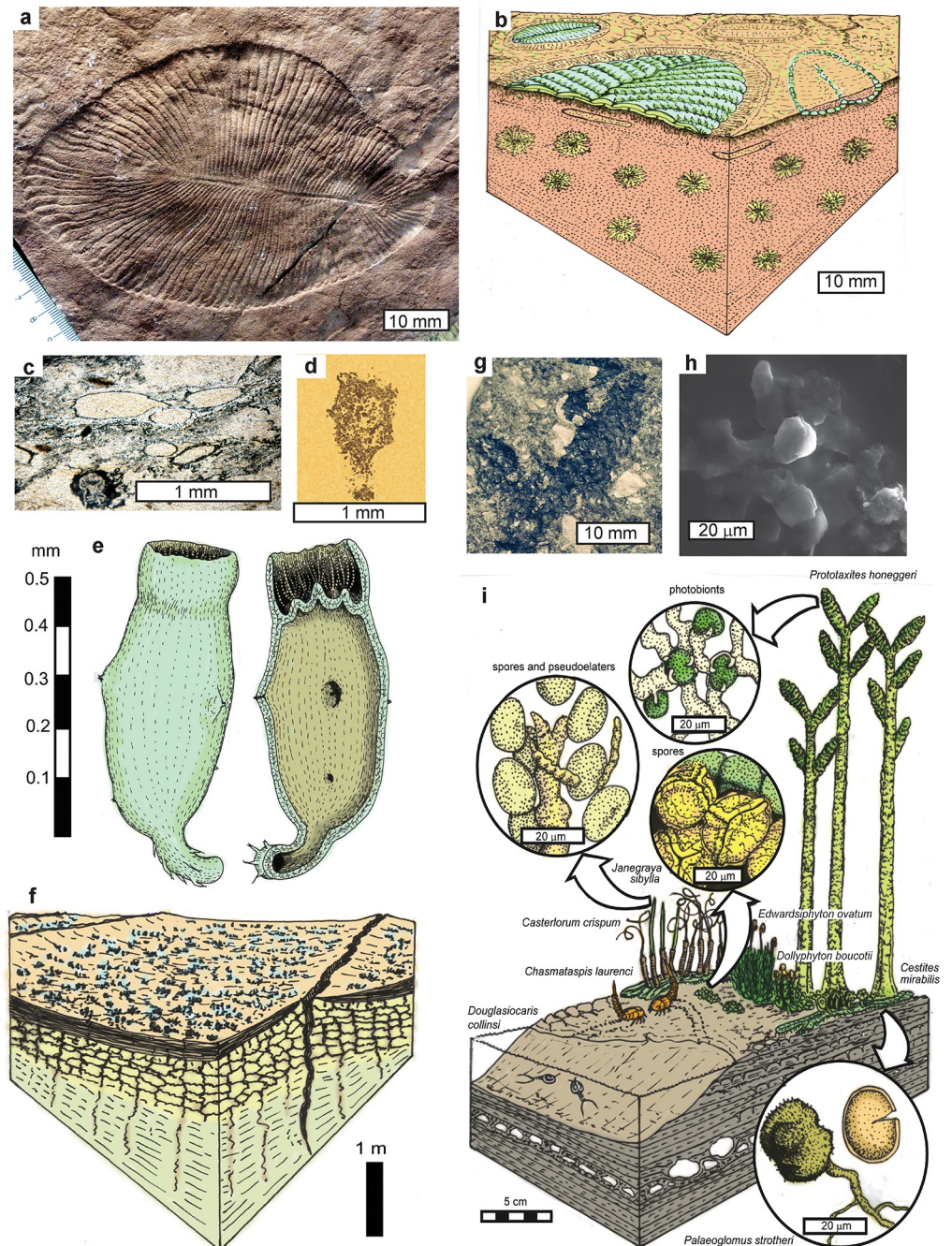


Fig 7. Comparison of *Dickinsonia costata* (a-b), with other extinct lichens, *Diskagma buttonii* from the Palaeoproterozoic (2.1 Ga) upper Hekpoort Basalt near Waterval Onder, South Africa (c-f), and *Prototaxites honeggeri* from the Middle Ordovician (Darrivilian or 460 Ma) Douglas Lake Member, Lenoir Limestone near Douglas Dam, Tennessee (g-i): a, hand specimen; b, reconstruction with *Phyllozoon hanseni* and *Aulozoon* based on thin section study [43, 48]; c, thin section; d, computed x-ray tomography image; e, reconstruction; f, reconstructed paleosol colonized by *Diskagma* [169]; g, branching apex; h, coccoid photobionts gripped by hyphae; i, reconstructed paleosol and associated fossils [85].

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to be attached to the characteristic nematophyte thallus. Dikaryan affinities are unlikely for small pencil-sized *Prototaxites* of Ordovician age [85], predating other evidence for Dikarya (Nelsen et al., 2020). By this comparison, *Dickinsonia*'s internal chambers, or "pneu structure" [16], demonstrated in thin section [48], would be comparable with cortical nests of *Prototaxites* [171]. This model for *Dickinsonia* matches the observed relative abundance of green algal stigmaterol and fungal cholesterol in *Dickinsonia* specimens of different inferred individual age [151, 162]. Declining stigmaterol to cholesterol proportions with age are compatible with fungal growth by regulation of green algal photobionts, rather than progressive fouling by algae of an animal, or environmental infiltration. Uncertainty comes from suspected modern contamination of *Dickinsonia* steranes [149, 163].

By either a *Diskagma* or *Prototaxites* model for *Dickinsonia* and other vendobionts, Kingdom Vendobionta [16], demoted to a Class Vendobionta [4], is best placed in fungal divisions Glomeromycota or Mucoromycotina.

Why was *Dickinsonia* considered marine?

The principal reason why *Dickinsonia* was first considered marine is because Reginald Sprigg, an enthusiastic scuba diver, thought that it looked like sea jelly [173]. This brought him into conflict with his former thesis advisor Sir Douglas Mawson, who also noticed these fossils as enigmatic markings during section measuring [174], but thought that the sandstones were fluvial and associated siltstones were loess [134]. A compromise suggestion of Sprigg, vividly portrayed by Glaessner [175], had them thrown up on the beach by storms. The culmination of this thinking was Peter Trusler's wonderful reconstruction of *Dickinsonia* as a multicolored worm in shallow oligotrophic tropical waters, an image also featured on Australian postage stamps [98]. Evidence against relationships between *Dickinsonia* and modern marine invertebrates was introduced by Seilacher [16]. Coastal plain and lagoonal habitats were envisaged for *Dickinsonia* by Jenkins et al. [115] and Gehling [116], until the idea that they lived in soils was published [63]. Immediately after that the sedimentary facies of *Dickinsonia* were reinterpreted as entirely subtidal [117, 176], for five reasons: (1) morphological complexity of vendobionts; (2) ripple marks interpreted as marine; (3) massive sandstones interpreted as submarine grain flows; (4) co-occurrence with sea-weed fossils; and (5) similar fossils in China and Australia interpreted as a single marine biotic province. *Dickinsonia* does indeed have regularity of module width and number [42, 45, 93], but lichens and mushrooms also have regularity of form if not damaged (Fig 3D–3F) [10]. Ripple marks form in a variety of marine, lacustrine and fluvial environments, including floodplains [130]. Massive sandstones are not only found in the sea, but deposited by river floods [177, 178]. Algae and other flimsy aquatic plants are fossilized with fossil plants in flood deposits [179, 180]. Plant and lichen remains are also preserved intact within marine and lacustrine deposits [181–183]. China and Australia were closer to each other in the Ediacaran than subsequently [8], at distances allowing shared marine and terrestrial species, judging from Phanerozoic paleogeographic distributions [184].

Conclusions

Ediacaran *Dickinsonia* specimens from Russia show damage and regeneration that challenges ideas about how they grew, and their biological affinities. A marginal and terminal disrupted zone of wilting forms a necrotic zone separating a regenerated portion, here called an antidel-toidal tag, sometimes on two diverging axes rather than a single axis. The nature of the antidel-toidal necrotic zone and tag are unlike posterior subterminal regrowth, as in trilobites. The necrotic zone and tag is also unlike regeneration of a posterior tail, as in annelids or millipedes. More likely *Dickinsonia* grew from a deltoid holdfast and elongated by growth from a

microscopic antideltoidal apical meristem, which repaired sublethal damage from freezing, salt or sunburn. This meristematic pattern of regrowth found in fungi and plants, is also comparable with growth of other Ediacaran fractal fossils such as *Fractifusus* and *Charnia*. When the apical meristem was damaged within the disrupted zone, lateral meristems formed one or two leaders of antideltoidal tags. The necrotic zone of damage to *Dickinsonia* is not inflamed, like an infection or frostbite. Nor is it a thick scar or callus, like an amputation. Nor is it a smooth transition to a regenerated limb. The wilted necrotic zone is most like damage by freezing, salt, or sunburn of leaves and lichens, compatible with evidence from associated frigid and gypsic paleosols for life on dusty periglacial soils. *Dickinsonia* grew and regenerated more like fungi and plants, than like animals, and can tentatively be placed within the fungal phyla Mucoromycotina or Glomeromycota.

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