

Review Article

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Following the logic behind biological interpretations of the Ediacaran biotas

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Abstract

For almost 150 years, megascopic structures in siliciclastic sequences of terminal Precambrian age have been frustratingly difficult to characterize and classify. As with all other areas of human knowledge, progress with exploration, documentation and understanding is growing at an exponential rate. Nevertheless, there is much to be learned from following the evolution of the logic behind the biological interpretations of these enigmatic fossils. Here, I review the history of discovery as well as some long-established core members of widely recognized clades that are still difficult to graft on to the tree of life. These ‘orphan plesions’ occupy roles that were once held by famous former Problematica, such as archaeocyaths, graptolites and rudist bivalves. In some of those cases, taxonomic enlightenment was brought about by the discovery of new characters; in others it required a better knowledge of their living counterparts. Can we use these approaches to rescue the Ediacaran orphans? Five taxa that are examined in this context are *Arborea* (Arboreomorpha), *Dickinsonia* (Dickinsoniomorpha), *Pteridinium* plus *Ernietta* (Erniettomorpha) and *Kimberella* (Bilateria?). With the possible exception of *Dickinsonia*, all of these organisms may be coelenterate grade eumetazoans.

1. Introduction

Most of the early discoveries of Ediacaran fossils were serendipitous (Richter, 1955; Ford, 1958; Anderson & Misra, 1968; Keller & Fedonkin, 1976; Minicucci, 2017), but Reg Sprigg (1919–1994) was actually looking for early animals when he found the holotype of *Ediacaria flindersi* (Fig. 1) at Ediacara in March 1946 (Sprigg, 1947, 1988). Furthermore, he found just what he and the World had expected: a jellyfish from the ‘age of jellyfishes’ (Sprigg, 1949, p. 97) – a concept that may have been influenced by C. D. Walcott’s monograph *Fossil Medusae* (Walcott, 1898), the report of a probable jellyfish, *Brooksella canyonensis*, from the Neoproterozoic Nankoweap Formation of the Grand Canyon (Bassler, 1941; Glaessner, 1962) and possibly by Gürich’s (1933) report of half a jellyfish (*Paramedusium africanum*) from the Nama beds of southern Africa. Sprigg was undoubtedly also encouraged by Kenneth Caster’s comprehensive report of a new fossil jellyfish (*Kirklandia texana*) from the Cretaceous of Texas (Caster, 1945), which he referenced in 1949. Almost all of these objects are now thought to be either trace or pseudofossils (Fürsich & Kennedy, 1975; Runnegar & Fedonkin, 1992). Nevertheless, Sprigg’s jellyfish hypothesis for the nature and mode of preservation of some of the most abundant Ediacaran fossils was widely influential for nearly 50 years, both in Australia (Glaessner, 1961, 1984; Wade, 1972b; Oliver & Coates, 1987; Jenkins, 1989) and in the Soviet Union (Fedonkin, 1985a, 1987). How did Sprigg’s jellyfish hypothesis arise and remain viable for so long? What other major hypotheses have been advanced to explain the Ediacara fauna? How have tradition, national proclivities and innovative thinking helped or hindered our understanding of the true nature of the Ediacara biota? These are some of the matters that are explored in this article.

2. Ediacaran hypotheses**2.a. Sprigg’s jellyfish hypothesis (1947+)**

Sprigg’s exposure to dehydrating jellyfish on Adelaide’s fine beaches (Sprigg, 1989) preconditioned his assignment of *Ediacaria* and other discoidal ‘medusoids’ to the cnidarian classes Hydrozoa and Scyphozoa. Not realizing that the invariably convex discs were on bed bases rather than bed tops, he saw them as jellyfish stranded by tides. This powerful imagery was adopted by Martin Glaessner when he moved to the University of Adelaide and began working on the Ediacara fauna (Fig. 1) and was inherited by Glaessner’s successor – Richard Jenkins – and Glaessner’s students, despite clear evidence for bed base preservation and subtidal deposition (Gehling, 2000; McMahon *et al.* 2021). It was Jim Gehling’s reinterpretation of the environment of deposition of the Ediacara Member (Gehling, 2000) and his work with

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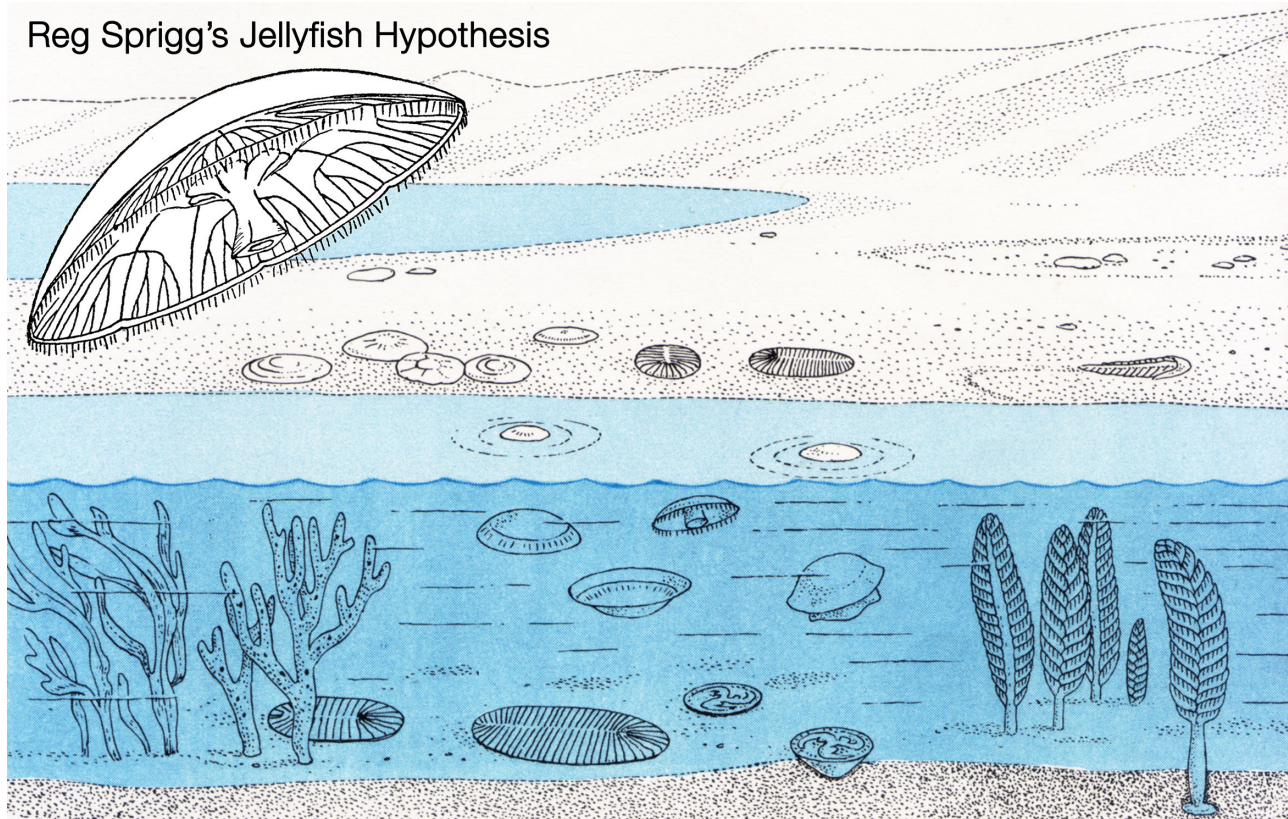


Fig. 1. Martin Glaessner's illustration of Sprigg's jellyfish hypothesis for the nature of the common Ediacaran fossils and their environment of deposition at Ediacara, South Australia plus his own Pennatulacea hypothesis, including a manifestation of Ford's chimera (Fig. 2, bottom right). Insert at upper left is Sprigg's reconstruction of the scyphozoan jellyfish *Ediacaria flindersi*. After Glaessner (1961) and Sprigg (1949, fig. 3B); © Bunji Tagawa 1961, republished with permission and with a Creative Commons Licence, respectively.

Guy Narbonne on the true nature of *Aspidella* Billings, 1872 (Gehling *et al.* 2000) that ultimately killed the jellyfish hypothesis. Nevertheless, before it died Ediacaran 'medusoids' had been confidently placed in most extant and many extinct medusozoan classes: Hydrozoa, Scyphozoa, Cubozoa, Conulata, Dipleurozoa, Cyclozoa, Inordoza, Trilobozoa (Sprigg, 1949; Harrington & Moore, 1955; Glaessner & Wade, 1971; Wade, 1972b; Jenkins, 1984; Sun, 1986; Fedonkin, 1987; Oliver & Coates, 1987). It is sobering to appreciate that four classic Ediacaran jellyfish – *Ediacaria* Sprigg, 1947 (Scyphozoa), *Cyclomedusa* Sprigg, 1947 (Cyclozoa), *Protodipleurosoma* Sprigg, 1949 (Hydrozoa) and *Irridinitus* Fedonkin, 1983 (Inordoza) – are no more than preservational variants of the holdfast of a single species of *Arborea* Glaessner & Wade, 1966 (Ivantsov, 2016).

2.b. Glaessner's Pennatulacea hypothesis (1959+)

Martin Glaessner (1906–1989) and Curt Teichert (1905–1996) were the first palaeontologists to view and collect Ediacaran fossils in South Australia. Both examined the holotype of *Ediacaria flindersi* during an ANZAAS meeting in Adelaide in August 1946, and Teichert travelled with Sprigg and his wife to Ediacara in 1947. However, it was Glaessner rather than Teichert who seized the opportunity after he moved to the University of Adelaide in 1950.

Sprigg's jellyfish hypothesis was supplemented by two major embellishments during the 1950s. Remarkably they came from discoveries in all three of the now recognized Ediacaran associations: Avalon (Charnwood), White Sea (Ediacara) and Nama (Namibia)

(Gehling & Droser, 2013). Working with newly collected material from Namibia, Rudolf Richter (1881–1957) showed that *Pteridinium simplex* Gürich, 1933, which had previously been thought to resemble a fern, was constructed of three separate vanes, each being formed of tubular modules (Richter, 1955). As the only living animals having this kind of triradial geometry are gorgoniid octocorals, the cnidarian or 'coelenterate' affinity of Ediacarans received additional support. Then in 1958, Trevor Ford (1925–2017) reported Roger Mason's discovery of *Charnia* and *Charniodiscus* in England (Fig. 2). At the time, Ford preferred an algal rather than an animal affinity for these two fronds but reluctantly yielded to a letter Glaessner published soon afterwards in *Nature* entitled 'Precambrian Coelenterata from Australia, Africa and England' (Glaessner, 1959b; Ford, 1980). According to Glaessner, the taxa we now know as rangeomorphs and arboreomorphs were pennatulacean octocorals and thus both highly derived cnidarians but also colonies that had achieved a high degree of integration that allowed them to act as collective 'individuals' (Dewel *et al.* 2001). This concept of complex coloniality was elaborately developed by Hans D. Pflug as the Petalonamae hypothesis for the common taxa of the Nama Association (Pflug, 1966, 1970, 1971, 1972a).

2.c. Pflug's Petalonamae hypothesis (1966+)

Glaessner had a couple of opportunities to doubt his own pennatulacean hypothesis but his belief in it may have overwhelmed his objectivity: a lesson for us all. As a native German speaker, he had read Gürich and Richter's descriptions of *Pteridinium* carefully

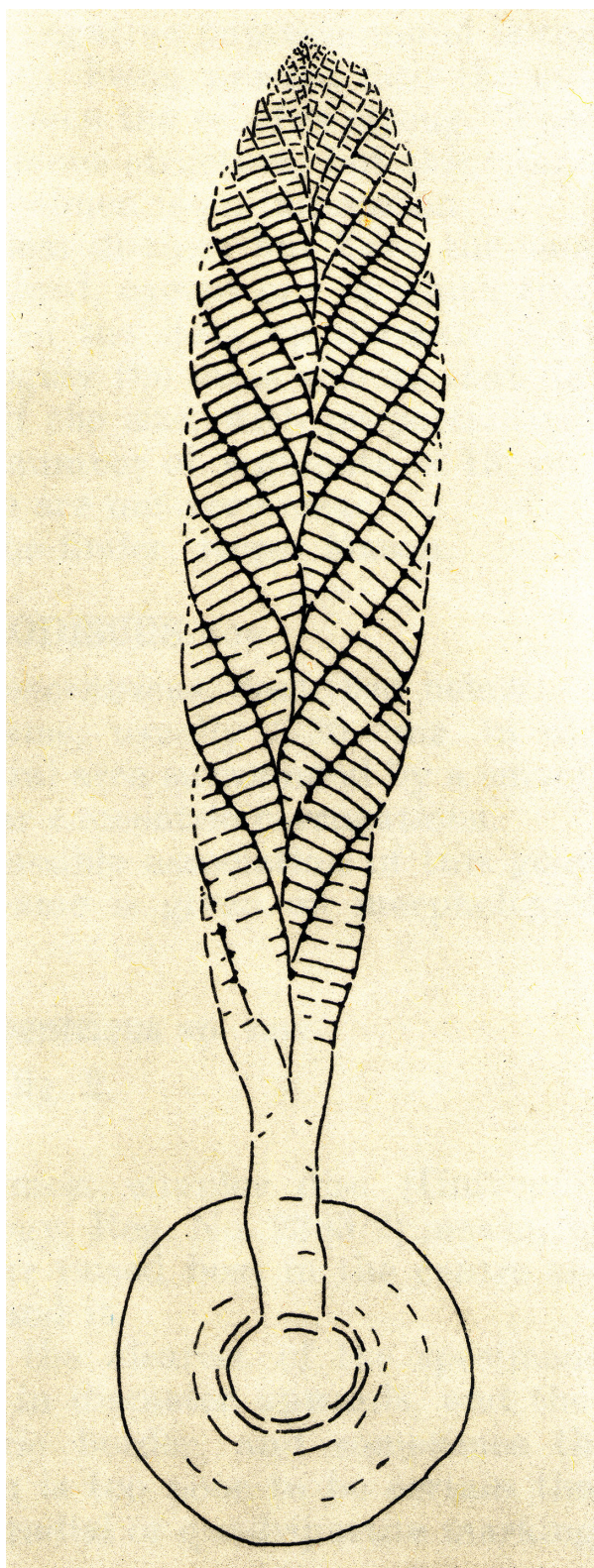


Fig. 2. Trevor Ford's chimera based on the frond of the rangeomorph *Charnia* and the holdfast of the arboreomorph *Charniodiscus* bridges the gulf between the two clades; both from the North Quarry of the Charnwood Golf Course, Leicestershire, UK, a locality discovered by Roger Mason in 1957 (Ford, 1958, fig. 3); © Yorkshire Geological Society 1958, republished with permission.

and was intimately familiar with fine specimens from Aar figured by Richter (1955), which he compared with small collections from the same site lent to him by the Geological Survey of South Africa and the Museum of Southwest Africa, Windhoek. Even so, he made no mention of the possibility of a third vane and instead emphasized similarities between *Pteridinium* and 'Rangea' (= *Arborea*), including his erroneous idea that both had primary and secondary orders of ribbing. He concluded that *Pteridinium* was a member of the Pennatulacea belonging to Richter's extinct family Pteridiniidae, *incertae sedis* (Glaessner, 1959a, 1963).

The second opportunity followed Mary Wade's 1964 discovery of a few fragments of *Pteridinium simplex* in a mass flow channel deposit at Ediacara. This Nama-style preservation was unique for South Australia, and neither Glaessner nor Wade seems to have realized that their best specimen (Glaessner & Wade, 1966, pl. 101, figs 1–3) shows clear evidence for three vanes. Unsurprisingly, they also concluded that *Pteridinium* and *Rangea*, as well as *Arborea*, were members of the Pennatulacea. However, only a few months earlier, Pflug (1966) had described another small collection from Aar Farm and had begun to build a radically different hypothesis based initially on shared features of *Pteridinium* and his new genus, *Ernietta* (Fig. 3).

For the Petalonamae hypothesis, Pflug merged the morphology of average specimens of *Ernietta* with deformed U-shaped individuals of *Pteridinium* that had been transported and buried by storm surge sands at the Aar *Lagerstätte* locality (Meyer *et al.* 2014b, figs 3–5; Pflug, 1970, pl. 23, figs 1, 3; Richter, 1955, pl. 7, fig. 11). In his mind – and if I have it right – the bag-shaped body (corpus) was formed of leaves or vanes (petaloids) made from co-aligned tubular modules, each of which housed an individual (persona) of the colony. Branching of the modules was sympodial rather than dichotomous, opposite, alternate or monopodial, resulting in zig-zag junctions between adjacent petaloids. In some forms the petaloids were replicated like the layers of an onion and adjacent petaloids or sets of petaloids curved to enclose a 'petaloid cavity' (centrarium). Channels between sets of petaloids (petalodia) served as gullets. Clade disparity was summarized using five shape categories and five alternative positions for the 'ingestion aperture' (Pflug, 1972a, table 1).

Richard Jenkins demolished this house of cards with the pithy statement: 'One of us (Jenkins) has examined Pflug's material and considers that all the specimens he refers to as the "Erniettomorpha" belong to a single genus and species, *Ernietta plateauensis* Pflug' (Jenkins *et al.* 1981, p. 71). Pflug's theories would retain only academic interest except for the fact that he was a fine observer, so his drawings and descriptions are a major resource. However, maybe his concept of a centrarium is not as crazy as it seems and is worth a second look?

Gibson *et al.* (2019, 2021) built a life-sized numerical model of an *Ernietta* from Aar and then used computational fluid dynamics and flume experiments with a 3D-printed version of the flask-like model to investigate how *Ernietta* might have used ambient water motion in feeding. They concluded that the observed gregarious growth allowed nutrient-rich water to preferentially enter the body cavity (Pflug's centrarium), which was 'likely the location of nutrient acquisition' (Gibson *et al.* 2021, p. 146). This process of an animal co-opting a piece of the external environment to develop a metabolically useful internal body cavity may be widespread. It was or is realised to lesser or greater extents in



Fig. 3. (a) *Ernieetta plateuensis*, Lower Member, Wood Canyon Formation, near Johnnie, Nevada, USA, specimen collected by Robert Horodyski, UCLA L7333-4; scale bar = 1 cm. (b, c) 3D models of *Ernieetta* with tapered growing module tips and plane of symmetry parallel to the axial seam. (d) Model of the base of *Ernieetta* shown in (c) has been reduced to nearly zero thickness in the Z direction to illustrate the topological relationship between (c) *Ernieetta* and (d) *Phyllozoon*.

the atria of sponges and archaeocyaths, the cnidarian coelenteron, the bilaterian gut, the molluscan mantle cavity, the water vascular system of echinoderms, the chordate branchial basket, the marsupial pouch and the human lung. We could even extend the concept to the covid pod, if we were to go beyond the body. Thus, the centrium of *Ernieetta* could be part of a pathway to the coelenteron, as discussed in Section 6.c.

Pflug thought that the ancestral petalonamid might have resembled the colonial ciliate *Zoothamnium* (e.g. Bright *et al.* 2019). From there he saw a transition through *Arborea* and *Charnia* to *Rangea*, *Pteridinium* and *Ernieetta* with much complexity added by preservational variants of each type. Here, I limit Petalonamae to three clades, Arboreomorpha, Rangeomorpha and Ernieetomorpha (Erwin *et al.* 2011), and treat dickinsoniomorphs under ‘Proarticulata’ (*contra* Hoyal Cuthill & Han, 2018).

2.d. Seilacher’s Vendozoa hypothesis (1983+)

Dolf Seilacher (1925–2014) was struggling with understanding the Ediacaran organisms as early as 1976, when we began the discussion during a trip to the trace fossil-rich marine Permian of the southern Sydney Basin, initiated and organized by Bruce McCarthy, during the International Geological Congress (Cooper & Branagan, 2015). At that time, Seilacher thought that they may have been megascopic prokaryotes. I remember well his subsequent presentation at the annual meeting of the Geological Society of America in Indianapolis in 1983, where he aired the Vendozoa concept, and Stephen Jay Gould’s enthusiastic reaction to it, despite the fact that Gould (1941–2002) was suffering severely from treatment for mesothelioma. The rest is history, but Gould served well as Seilacher’s bulldog in promoting the vendozoan hypothesis (Gould, 1984).

Seilacher tried to place all of the soft-bodied Ediacaran organisms in a single clade, but even he had to allow some exceptions, most notably for the ‘sand corals’ (Psammocorallia) and the trace fossils (Seilacher, 1989, 1992). Originally conceived as something akin to stem lineage animals, vendozoans soon became vendobionts with their affinities transferred to the rhizopodan protists, specifically foraminiferans and xenophyophores (Seilacher, 1992, 2003). These kinds of alveolates are now far removed from the Opisthokonta, which includes the animals and fungi, but their supergroup (TSAR) is closer to the Archaeplastida (a.k.a. ‘plants’) than to the supergroup containing the opisthokonts (Amorphea; Burki *et al.* 2020). In that sense, both Petalonamae and Vendobionta conform to the notion of an extinct kingdom somewhere between animals and plants, which was what Pflug thought.

Other aspects of the vendozoan hypothesis can also be traced to Pflug’s ideas, although the Petalonamae were specifically excluded from the original proposal (Seilacher, 1989, p. 237). Both Pflug and Seilacher emphasized the modular construction for tubular units as the unifying feature of this extinct clade and the mechanism that allowed growth to proceed to larger body sizes than had previously been possible.

2.e. Fedonkin’s Proarticulata hypothesis (1985+)

The holotype of *Dickinsonia* is incomplete so, with the jellyfish hypothesis in mind, Sprigg reconstructed it as being ‘symmetrical across both longitudinal and transverse planes’ (Sprigg, 1947, p. 222). Even though this was clearly untrue after Sprigg’s second description of the fauna (Sprigg, 1949), Harrington & Moore

(1955) still made *Dickinsonia* the only known example of their new coelenterate class Dipleurozoa. Perceptively, Glaessner thought that *Dickinsonia* ‘resembles certain worms more than any coelenterate’ (Glaessner, 1958, 1959a; Glaessner & Daily, 1959, p. 379). This idea was firmed up soon afterwards using comparisons of *Dickinsonia* and *Spriggina* Glaessner, 1958 with the highly derived extant polychaetes *Spinther* and *Tomopteris*, respectively (Glaessner, 1959a, 1961). Perhaps stimulated by Sidnie Manton’s (1902–1979) lead article on *Spinther* in the new *Journal of Natural History* (Manton, 1967), Mary Wade (1928–2005) promoted *Dickinsonia* as a primitive polychaete ‘derived from ancestors with biramous parapodia and a more normal, elongate shape’. This idea was falsified by Runnegar (1982) who showed that, unlike *Spinther*, *Dickinsonia* did not develop its discoidal shape from a vermiform juvenile growth stage (Zakrevskaya & Ivantsov, 2020).

Dickinsonia was discovered on the Onega Peninsular of the White Sea coast of Russia by M. A. Fedonkin in the summer of 1975 (Keller & Fedonkin, 1976). Better specimens obtained during the next decade suggested that the animal was not precisely bilaterally symmetrical. Rather, its segments alternated across the midline producing what has become known as ‘slide’ or ‘glide’ symmetry (Fig. 4). This is something like the zig-zag axial junctions of the petaloids of Pflug’s erniettomorphs, but was generally interpreted in Russia as offset metamerism rather than mere geometric packing. In 1985, Fedonkin (1985b, 1998) proposed the new phylum Proarticulata to house *Dickinsonia* (Class Dipleurozoa), *Vendia* Keller, 1969 and related forms. Since then, Andrey Ivantsov and his colleagues have greatly expanded our knowledge and understanding of this proarticulate clade and the putative trace fossils associated with some of its members (Ivantsov, 1999, 2004, 2007, 2011, 2013; Ivantsov & Malakhovskaya, 2002; Ivantsov *et al.* 2019a,b,c; Ivantsov *et al.* 2020; Ivantsov & Zakrevskaya, 2021a).

At the time Proarticulata was proposed, similarities in the segmentation of annelids and arthropods were still being used as evidence for their common ancestry (Scholtz, 2002). Now that it is clear that Articulata (Annelida + Arthropoda) is not a valid group, it is trivially easy to reject the Proarticulata hypothesis (Dunn & Liu, 2019). However, maybe this is throwing out the baby with the bathwater; a better approach may be to ask whether the repeated isomers/modules/units of the proarticulates share any pattern-forming processes with those controlling segmentation in annelids, arthropoda and chordates. It has become clear that segmentation in those clades evolved convergently (Seaver, 2003; Chipman, 2010; Evans *et al.* 2021). However, seriation of some sort must have a long history in all three main bilaterian clades. For example, early branching panarthropods such as *Aysheaia* Walcott have stereotypical sets of annulated lobopodial limbs (Chipman & Edgecombe, 2019), implying that earlier vermiform ecdysozoans had probably already acquired the axial patterning that could be co-opted for generating appropriately spaced legs, as envisaged by Erwin (2020). These possibilities are explored below.

3. Age and duration of the Ediacara biota

When I entered the University of Queensland early in 1959, Dorothy Hill (1907–1997) began the palaeontology lectures with the then prevalent first approximation that there was no evidence

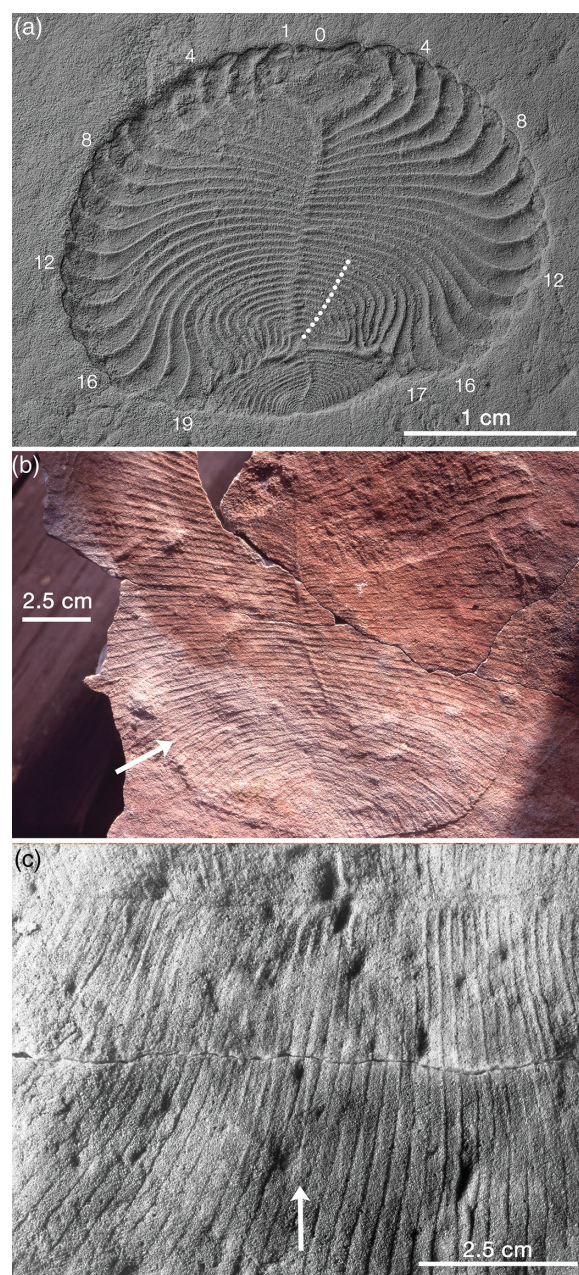


Fig. 4. Anatomical details of *Dickinsonia*. (a) Beautifully preserved specimen of *D. cf. menneri* that survived a non-lethal injury and regenerated its tailpiece. The first 17 modules grew normally but the following 13 modules (white dots) were damaged and then grew abnormally (in some cases joining up distally); a new tailpiece was generated from the axis and grew in such a way as to rebuild the oval body outline. Note that although some modules appear to be offset across the midline, others are clearly not offset, and the same number of modules occurs on both sides of the body; RAS PIN 4716/5187, Lyamtsa Formation, Onega Peninsula, Russia, image courtesy of A. Yu. Ivantsov. (b) Unusually large incomplete specimen of *D. costata*, which displays evidence for both upper and lower surfaces, as shown by the Y-shaped intersections of the module walls (arrow), and it illustrates the ambiguity frequently seen in proarticulates with respect to glide symmetry versus strictly bilateral symmetry; SAM P58615, Ediacara Sandstone Member, Rawnsley Quartzite, Parachilna Gorge. (c) Part of complete specimen of *D. costata* that also shows both surfaces; arrow points to one of several ridges that reflect one surface of the organism whereas the grooves they cross at a small angle represent the other surface; Sperling & Vinther (2010, fig. S1) identified this specimen as *Dickinsonia rex* and regarded it as a ‘footprint’, not a body fossil; SAM P58616, Ediacara Sandstone Member, Rawnsley Quartzite, Ediacara, South Australia.

for life before the Cambrian; the preceding ~3.5 billion years of Earth history were 'Azoic'. The tide, however, had already turned; Ford's (1958) article on the Precambrian age of *Charnia* and *Charniodiscus* was on its way to Australia by boat, and Glaessner's (1959b) letter to *Nature* was about to appear. Furthermore, Arthur Holmes' (1890–1965) final attempt at a radiometrically calibrated geological timescale, which estimated the base of the Cambrian to be 600 ± 20 Ma, would be published by the end of the year (Holmes, 1959). Fast-forward to the present. The base of the Cambrian is now constrained to be between 538.4 and 538.8 Ma based on recent U–Pb ages from Namibia and Mexico (Linnemann *et al.* 2019; Hodgkin *et al.* 2020); the oldest Ediacarans postdate the Gaskiers glaciation in American Avalonia at ~574 Ma (Pu *et al.* 2016; Matthews *et al.* 2021); and the acme of the Ediacaran biota (White Sea assemblage), measured in terms of both diversity and disparity, existed from >558 to <555 Ma.

4. FAQs (frequently asked questions)

4.a. Were the Ediacaran fossils lichens?

Greg Retallack had this 'annoying idea' in 1988 and found it surprisingly difficult to falsify (Retallack, 1992, 1994). Judging from the plethora of critiques his numerous articles dealing with this scenario have attracted, others have found it just as hard to accept. Here, we shall limit the discussion to five key elements of the lichen hypothesis: (1) Were the resistant Ediacaran organisms, which are preserved as external moulds on bed bases, woody like plants (Retallack, 1994)? (2) Are the Ediacaran fossils preserved in fossil soils (Retallack, 2012, 2013)? (3) Is the red colour of Australian Ediacaran sediments primary or secondary (Retallack, 2012)? (4) Did the Ediacaran organisms live on land, in the sea or both (Retallack, 2013, 2014)? (5) Were the Ediacaran organisms lichens or fungi (Retallack, 1994, 2007, 2016)?

(1) *Woody or not?* Wade's (1968) landmark paper on the preservation of the fossils at Ediacara set the stage for all subsequent work on this topic. She recognized the distinction between resistant animals, which are preserved as external moulds on the bases of beds, and non-resistant ones whose bodies collapsed upon burial. Perceptively, she attributed the formation of counterpart casts to upward movement of relatively incompetent sediment from the underlying bed. This process has been explored experimentally by Bobrovskiy *et al.* (2019). We might term it the *waterbed hypothesis*, one that requires a flexible but inextensible membrane (the mattress), the incompressible fluid it encloses and the bed frame, which holds the mattress in place (Press, 1978). At Ediacara, these could have been the microbial mat on which the organisms were living, the water-filled pore spaces beneath the mat and the laterally unbounded hydrostatic pressure within the sediment.

The principal alternative is the *death mask hypothesis* (Gehling, 1999), which requires early mineral cements (iron sulfides or quartz) to support the overlying bed during the decay of the organism (Tarhan *et al.* 2016; Liu *et al.* 2019). I prefer the waterbed hypothesis because it relies on conditions that may be regarded as ubiquitous, given the tight association between the fossils and the matgrounds on which they were preserved. Early mineralization fuelled by the decay of organic matter would have had to be remarkably selective to invariably distinguish between resistant and non-resistant organisms, whereas their different resistances to

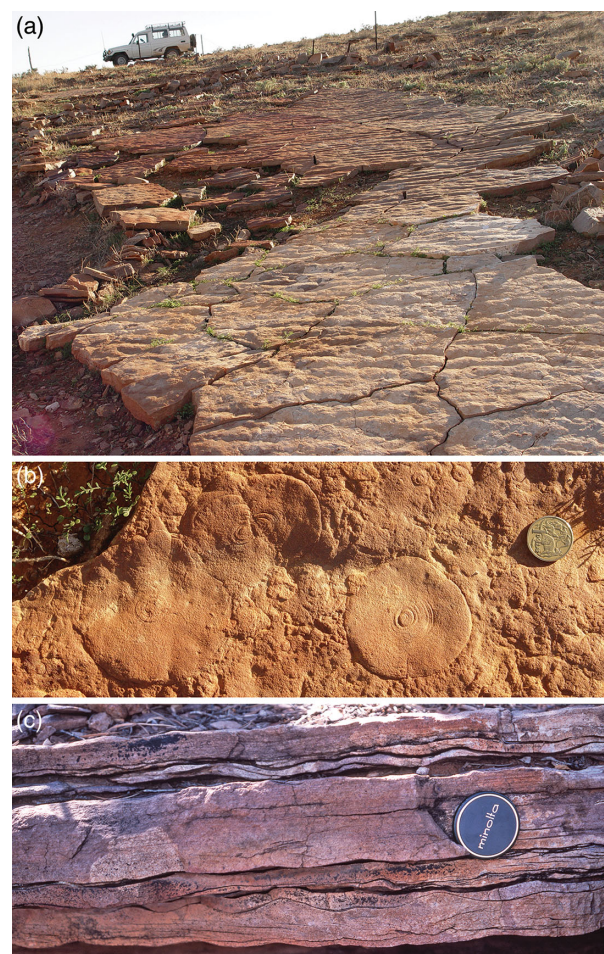


Fig. 5. Fossiliferous flaggy sandstones at the (a, b) Nilpena National Heritage Ediacaran fossil reserve and (c) Mt Scott Range, western Flinders Ranges, South Australia. Retallack (2016) considered these kinds of deposits to be palaeosols, formed on a braided stream floodplain ~60 km inland from the Ediacaran shoreline. The standard view is that they were deposited in a shallow marine environment below fair weather wave base. Overtuned bed in (a) is TC-MM3, the lower surface of which (b) is dominated by frond holdfasts (Droser *et al.* 2019). Seen in cross-section (c), these beds bear no resemblance to palaeosols. Coin in (b) and lens cap in (c) are 25 mm and 60 mm in diameter, respectively.

loading should have achieved that automatically. More experimentation is clearly needed. In any case, Retallack (1994) completely misunderstood the nature of the preservation of the resistant organisms when he compared them with various fossil woods (Waggoner, 1995). This argument for a lichen affinity is not sustainable.

(2) *Are the fossils on terrestrial soils or marine matgrounds?* This is a difficult question to address generally so the focus will be on three specific examples. The richly fossiliferous beds at the western edge of the Flinders Ranges (Nilpena, Ediacara, Mt Scott Range) are packages of thin, ripple-marked flaggy sandstones and even thinner intervening sandy 'shims' (Fig. 5; Tarhan *et al.* 2017). Retallack (2019, p. 64) considered these sites to have been ~60 km inland from the Ediacaran coast and attributed the shims to wind deposition during dry seasons. These clean, sandy quartzites (Fig. 5c) display no textural or chemical evidence for soil formation, so if the Ediacaran organisms were living on these barren braided floodplains, they were doing so in a nutrient-poor environment exposed to enhanced UV under an oxygen-depleted atmosphere (Li *et al.* 2020). The arboreomorphs, in particular, may

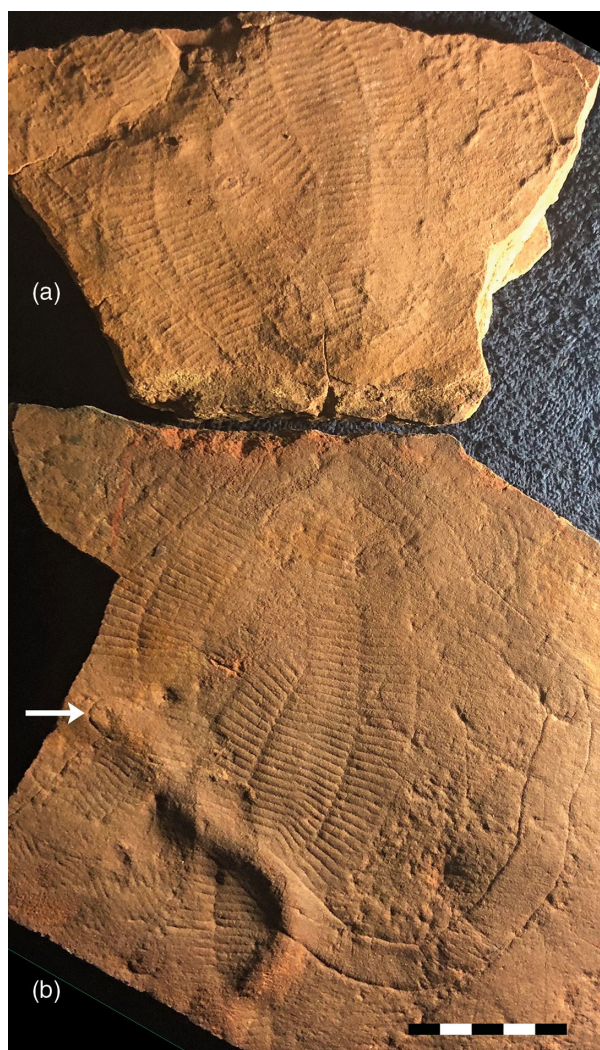


Fig. 6. Fronds of *Phyllozoon hansenii* and tubes of *Aulozoon soliorum* on a piece of a 3–4 cm thick event bed from Bathtub Gorge, central Flinders Ranges (Gehling & Runnegar, 2021). The counterpart (a) is the top of the A horizon of a Muru palaeosol according to Retallack (2013). Both event bed and ‘palaeosol’ are thin, laminated quartz sandstones; the terrestrial palaeosol interpretation is clearly falsified by this example. Arrow marks apparently closed end of one *Aulozoon* tube. Scale in centimetres. Image courtesy of J. G. Gehling.

have had a hard time. Yet they persisted, becoming as frequent as $\sim 60 \text{ m}^{-2}$ in this hostile situation (Droser *et al.* 2006). Alternatively, if these beds were produced by storm waves in a quiet subtidal setting (Gehling, 2000; Gehling & Droser, 2013; McMahan *et al.* 2021), life for the arboreomorphs should have been easier, as it presumably was beneath the photic zone in Avalonia (Wood *et al.* 2003). The extraordinary ecological range implied by identifying the Nilpena flaggy sandstones as fossil soils is one of the best reasons for rejecting the lichen hypothesis.

A second specific example is the ‘Muru pedotype’ found beneath a 3–4 cm thick event bed in Bathtub Gorge, central Flinders Ranges, that buried and preserved a death assemblage of *Phyllozoon* fronds, *Aulozoon* tubes and *Dickinsonia* footprints (Gehling & Runnegar, 2021; Retallack, 2013, p. SI4). In this case, the underlying, equally thin sandstone, which is covered with counterpart casts of fossils found on the base of the overlying event bed, is well lithified and easily extracted from the outcrop (Fig. 6). There is no textural or chemical evidence for the A, B and

C horizons of the type Muru pedotype (Fig. 6a, b). Suggestions that *Phyllozoon* was a window lichen and *Aulozoon* a mycelial rhizome, with *Dickinsonia* as its mushroom (thallus; Retallack, 2007), are imaginative but unrealistic, given the fact that the putative rhizomes are in the event bed that buried the organisms, not in the underlying ‘palaeosol’ (Fig. 6; Gehling & Runnegar, 2021).

The third specific example is from Brachina Gorge, central Flinders Ranges, the type locality for the Wadni and Muru pedotypes (Fig. 7; Retallack, 2012). As we know from political debates, facts are not necessarily enough to overcome deeply held beliefs. In this case, the one example that might help tip the balance is the preservation of *Dickinsonia*, *Parvancorina* Glaessner, 1958 and other taxa on the distended lower surfaces of large load casts at the base of a sandstone bed in Brachina Gorge, central Flinders Ranges (Fig. 7). According to Retallack (2012), this bed is the C horizon of the type section of his Muru pedotype and was deposited in a sandy river channel before being deformed, not by hydrostatic foundering, but by glacial ice moving over the A horizon loess. This special pleading is necessary to explain sedimentary structures that are otherwise readily attributed to liquefaction or fluidization in aquatic environments (e.g. Owen, 1996). Furthermore, the woody properties attributed to *Dickinsonia* under the lichen hypothesis (Retallack, 1994, 2007) are not expressed in the curvature of a sizeable individual preserved on the convex surface of one rounded load cast (Fig. 7e–g). In each of these examples, the sandstones underlying the fossils have no features of fossil soils and in two of the three cases (Nilpena and Bathtub Gorge) closely resemble sandstones that overlie the fossils. In the third example (Brachina Gorge), the ‘palaeosol’ is a red siltstone that is directly overlain by a thick quartz sandstone that has undergone soft-sediment deformation typical of shallow marine conditions (McMahan *et al.* 2021). There is little reason for regarding any of these sediments as terrestrial.

(3) *Are the red beds oxidized soils or just outback Australia?* Australia’s ‘red centre’ is legendary and the default explanation is regolith chemistry, which has oxidized an ancient landscape that in places may date back to the Mesozoic Era (Twidale, 2016). The difficulty of distinguishing between primary ferric components and those that have been generated by post-depositional processes is exemplified by the saga of the Marble Bar Chert (Rasmussen *et al.* 2014), where the red colour was for a time used to argue for an oxygen-rich Archaean atmosphere. The red silts in Brachina Gorge, which characterize the type Wadni and Muru pedotypes (Retallack, 2012, 2013), are far more likely to be the products of Cenozoic weathering than Ediacaran soil formation (Pillans, 2018).

(4) *Were the organisms terrestrial, marine or both?* Although Retallack has considered almost every fossiliferous Ediacaran deposit – even Avalonian Newfoundland (Retallack, 2014) – to be no deeper than intertidal, the credibility of his arguments diminishes with distance from South Australia. If the evidence there is equivocal at best, there is little in favour of a terrestrial habitat at any of the classic soft-bodied sites.

(5) *Do the fossils themselves resemble lichens or fungi more than animals or plants?* This question has been thoroughly explored (Lücking & Nelsen, 2018) and the definite answer is ‘no, they do not’. The lichen hypothesis is a false lead that has taken up too much space in the literature.

4.b. Were Ediacaran organisms colonial?

Rangea, *Charnia* and *Charniodiscus* automatically became highly individualized colonial animals by Glaessner’s (1959b) promotion

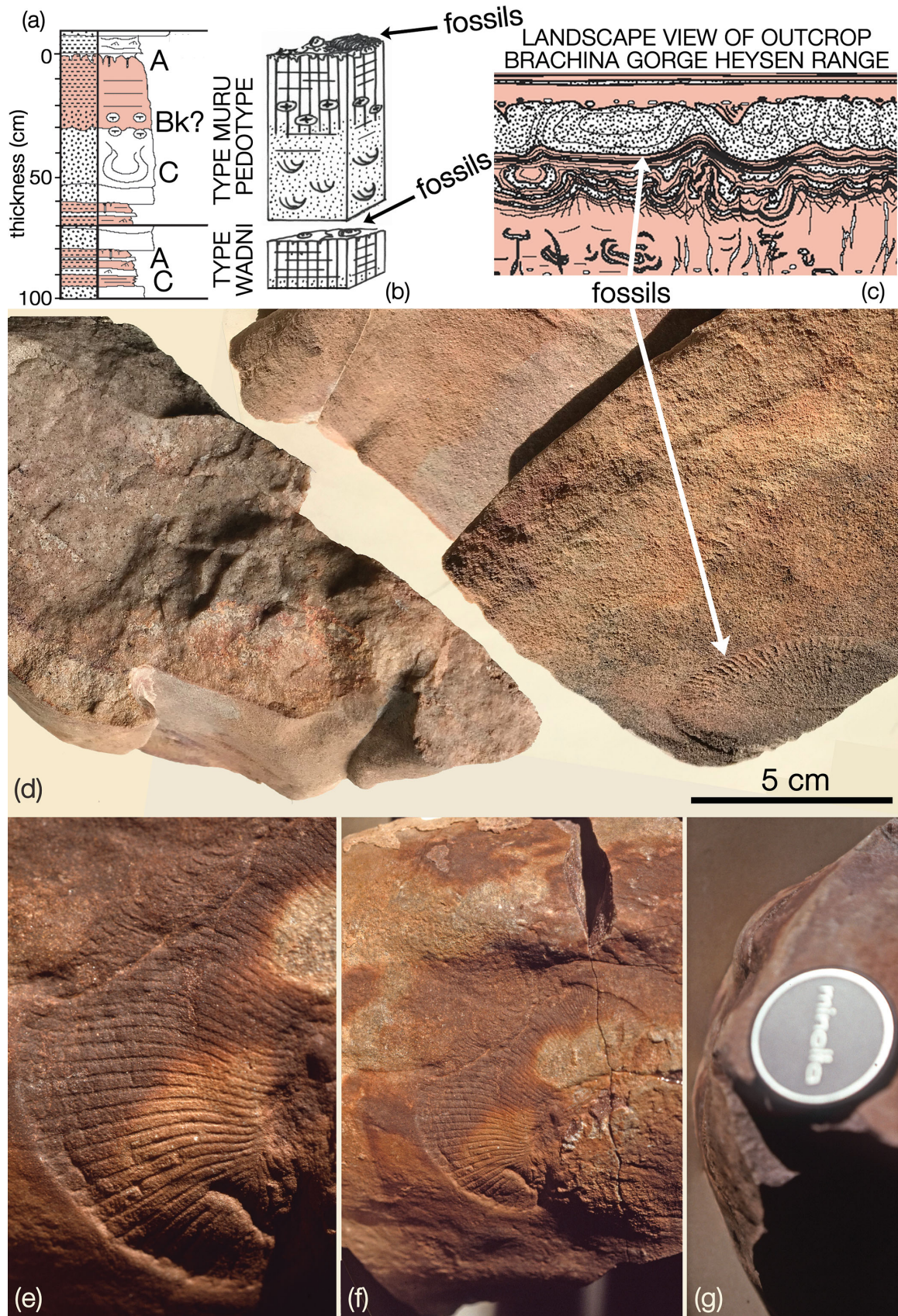


Fig. 7. (d–g) Negative hyporelief casts of *Dickinsonia costata* on deformed sandstone bed bases, Brachina Gorge, central Flinders Ranges and (a–c) Greg Retallack's interpretation of these surfaces as the base of the C soil horizon of the type section of the Muru pedotype; after Retallack (2012, fig. 14c) © John Wiley and Sons 2012, republished with permission; and Retallack (2013, fig. S2), reprinted by permission from Springer Nature: *Nature*, Ediacaran life on land, G. J. Retallack, Copyright (2012). This soft-sediment deformation is attributed to gravitational instability resulting from liquefaction or fluidization (Owen, 1996), which is easy to envisage in a shallow marine setting but harder to achieve on a terrestrial floodplain. The convexly curved *Dickinsonia* in (e) and (f) is on the surface of a load cast, seen in profile in (g); SAM P31895, 60 mm camera lens for scale. The *Dickinsonia* marked by the arrow in (d) is on the complexly folded bed base shown in profile (left) and in oblique view (right); SAM P34356.

of the pennatulacean octocoral hypothesis for these frondose forms from Avalonia, Namibia and Australia. This hypothesis was widely accepted (Jenkins, 1985; Oliver & Coates, 1987) until falsified after almost 50 years by Waggoner & Collins (2002) using a molecular clock, and by Antcliffe & Brasier (2006), who contrasted their modes of growth and development. Pennatulacean octocorals are highly evolved cnidarians, well removed from basal groups, so their ability to operate as innervated individuals is a derived feature of the clade. Nevertheless, by attributing this ability to many of the Namibian Petalonamae, Pflug (1971, 1972a) saw a transition from frondose taxa such as *Rangea* and *Arborea* to animal-like colonies with some of the attributes of echinoderms, arthropods, molluscs and even chordates. These fanciful ideas were based mainly on preservational variants of the three common Namibian genera – *Rangea* Gürich, 1930, *Pteridinium* and *Ernietta* – and have no relevance now other than historical interest. However, Dewel *et al.* (2001) advanced a much more sophisticated and well-received hypothesis along similar lines, using *Pteridinium*, *Charnia*, *Rangea* and *Arborea* as examples of the progress of colonial duplication and integration during Ediacaran time. In this scheme, the pennatulacean-level integration of *Arborea* allowed it to operate as a self-sufficient mobile individual and raised the possibility that animals such as *Dickinsonia* might show how colony integration led to bilaterian segmentation. However, as none of these organisms seems to have been colonial except in the most elementary way (Landing *et al.* 2018), colonialism *per se* was probably not the evolutionary pathway to more familiar animals (but see Ivantsov, 2016 for a different view). Nevertheless, life is built on the LEGO® Principle (McKay, 2004). Think elements, biomolecules, ribosomes, cells, organs, segments, individuals, populations, guilds, biomes. In this sense, it is *clonal* construction rather than *colonial* construction that characterizes the Ediacaran organisms.

4.c. How and what did Ediacaran organisms eat?

Seilacher (1989) had to confront this issue because he could not rely on the mechanisms that were available to those who viewed the Ediacarans as coelenterates, worms and arthropods. He assumed all nutrition needed to be absorbed through the body wall and speculated that the organisms may have depended on endosymbionts for their sustenance (McMenamin, 1986). He discussed the possibility of photosymbionts for upright taxa in shallow water and chemosymbionts for deepwater taxa and ‘mat recliners’. He even sketched out how endosymbionts in an organism like *Dickinsonia* could have exploited the oxic–anoxic interface of a matground, obtaining H₂S from below and oxygen from seawater. This remains a viable hypothesis for prostrate organisms (Gehling *et al.* 2005; McIlroy *et al.* 2021). The alternative for an almost sessile creature with no other food-collecting abilities is *in situ* ventral digestion of the kind used by the living placozoan *Trichoplax* (Sperling & Vinther, 2010).

For the upright fronds and many other forms, all of which have high surface-to-volume ratios, osmotrophy has been the feeding mode of choice (Laflamme *et al.* 2009; Ghisalberti *et al.* 2014). However, Butterfield (2020) has made a strong case against having the food absorbed from the outside and instead argued that it was taken in and processed inside, more or less as sponges and cnidarians do. As the food in question is thought to be either dissolved organic carbon (DOC) or particulate organic carbon (POC), I dub these two possibilities the DOC POOL (external feeding) and DOC POC (internal feeding) hypotheses (Fig. 8a). The Devonian rugose corals *Heliophyllum* and *Crepidophyllum*, which had digestive

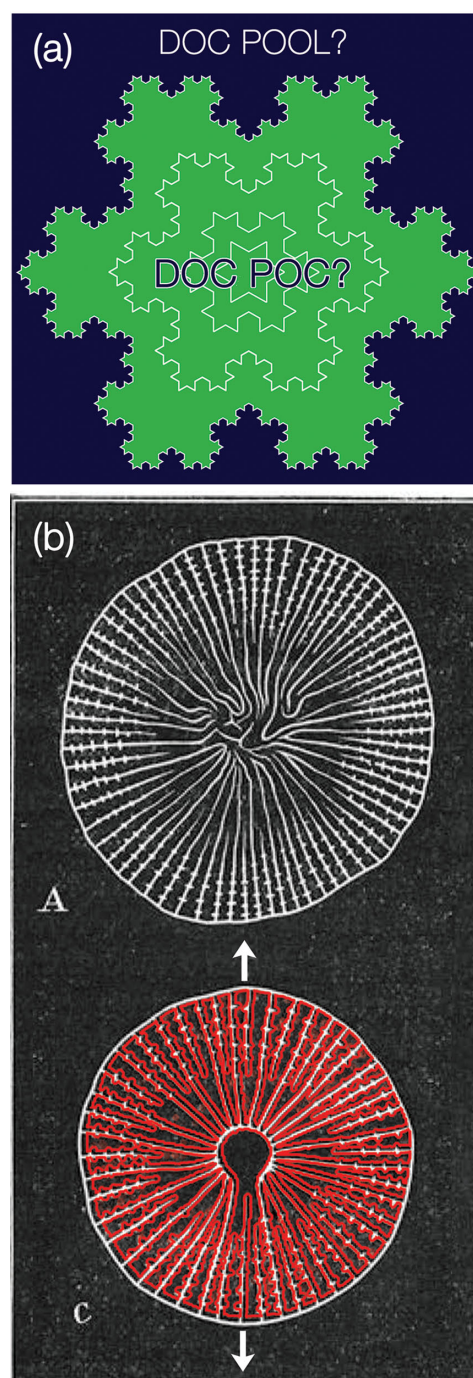


Fig. 8. Cartoons aimed at illustrating the high surface to area relationships of (a) epidermal cross-sections of rangeomorphs and (b) Devonian rugose corals. The nested curves in (a) are known as ‘Koch snowflakes’; they are produced by duplications and rotations of a Koch curve (McCartney, 2021). They simulate the increase in complexity with size displayed by rangeomorph fronds during growth (Narbonne, 2004b). The green area represents the interior of the largest shape, which might have contained and processed dissolved and particulate carbon (DOC, POC). Under the DOC POOL hypothesis, food is absorbed directly from ocean water (Laflamme *et al.* 2009); the DOC POC hypothesis assumes that food was taken in and processed internally (Butterfield, 2020). (b) Drawings of two transverse sections of the rugose corals (A) *Heliophyllum* and (C) *Crepidophyllum* illustrate how second-order ridges on major and minor carinate septa increase the area available for digestion by the gastrodermis (red). The directive axis of *Crepidophyllum* is indicated by arrows; this key-hole coral is shown in what was standard rugose coral orientation but should be rotated through 180° for comparison with other anthozoans (Oliver, 1980). From Nicholson (1878), reproduced with permission from <http://www.tandfonline.com>.

epithelium covering their carinate or ‘yard-arm’ septa (Fig. 8b), serve as possible analogues for Butterfield’s DOC POC mode. The ultimate origin of these postulated dispersed and degraded food resources may be provided by evidence from biomarkers (Bobrovskiy *et al.* 2020). However, the high density of substrate occupation by some frondose taxa (200–1000 m⁻²; Ivantsov, 2016) raises questions about supply. Another worry is the metabolic cost of keeping sizeable fronds inflated if Butterfield’s (2020) DOC POC hypothesis is correct.

Another insight into the nutrition of Ediacaran organisms may come from the stunning report of abundant derivatives of cholesterol in coalified cadavers of *Dickinsonia* at a White Sea locality (Bobrovskiy *et al.* 2018). Cholesterol is a molecule that stiffens the membranes of eukaryotic cells. It is the dominant sterol in metazoans but is found in lesser amounts in other eukaryotes, most notably red algae (Brocks *et al.* 2017). In an adult human, cholesterol forms about 0.33 % of total body weight so the amount present in any *Dickinsonia* carcass is likely to have been <1 %. In herbivores, all of the cholesterol may be assumed to have been produced *in situ*, but omnivores and carnivores acquire significant amounts via their diets. Thus, the biomarkers found in *Dickinsonia* have some potential for understanding both its affiliation and its metabolism. However, any metabolic interpretation is complicated by what happens to the biomolecules following excretion, ingestion, death, burial and diagenesis. In *Dickinsonia*, the most abundant fossil steroids (steranes) are 5- β cholestane (sometimes known as coprostanane) and its monoaromatic equivalents. This is surprising because most cholesterol is converted abiologically into 5- α cholestane, which is more stable and retains the *trans* stereochemistry of cholesterol and other natural steroids, unlike coprostanane. Diagenetic isomerization normally drives the 5- β /5- α ratio towards an equilibrium value of ~0.65, so ratios as high as 5.5 in the White Sea *Dickinsonia* compressions require explanation (Bobrovskiy *et al.* 2018).

In humans and some other animals, anaerobic bacteria can convert cholesterol in the gut into coprostanol – which dehydrates to coprostanane – either directly or via intermediates (Kriiaa *et al.* 2019). If this is what caused the elevated 5- β /5- α cholestane ratios in *Dickinsonia*, how did obligate anaerobes gain access to cholesterol? If *Dickinsonia* had a gut and digestive system (Ivantsov, 2011), cholesterol is unlikely to have been part of the diet as the only environmentally available sterol seems to have been stigmaterol from green algae and unicellular heterotrophs (Bobrovskiy *et al.* 2018, 2020). Most of the cholesterol in *Dickinsonia* must have come from its tissues and it is therefore necessary to implicate anaerobes in the decay process, something not seen in younger forensic, archaeological or palaeontological contexts (Melendez *et al.* 2013; von der Lühe *et al.* 2018). However, this was Bobrovskiy *et al.*’s (2018) preferred explanation for the elevated 5- β /5- α ratios.

Bobrovskiy *et al.* (2020) pointed out that unicellular eukaryotes are a far better food source for early animals than are bacteria and suggested that the availability of high nutritional quality algal biomass may have triggered the Ediacaran radiation of metazoans. The fact that algal stigmaterols were not found in *Dickinsonia* may perhaps be explained if the unicellular eukaryotes were digested intracellularly rather than being incorporated into an alimentary canal system; shrimp fed on algal sterols excrete them ‘qualitatively and quantitatively’ (Bradshaw *et al.* 1990). The same logic could be applied to explain the dearth of bacterial hopanes in *Dickinsonia*. Hopanes are the carbon skeletons of hopanoids, which some bacteria use instead of steroids to stiffen their cell membranes;

the hopane/sterane ratio of the fossils is ~0.5 (Bobrovskiy *et al.* 2018, table S3) compared with the enclosing sediments, which have a ratio of ~3 (Bobrovskiy *et al.* 2020, table S1). Thus, it seems that the biomarker evidence supports a lifestyle based on poriferan-style phagocytosis rather than bilaterian extracellular digestion (Steinmetz, 2019); the former would destroy membrane molecules cell-by-cell soon after ingestion (see also McIlroy *et al.* 2021).

The other principal hypothesis for vendobiont nutrition, endosymbiosis, may also be examined from the biomarker perspective. If *Dickinsonia* had been packed full of bacterial chemosymbionts like the trophosome of the vent worm *Riftia pachyptila* (Jones, 1981; Bright & Sorgo, 2003), then their presence should be reflected in the hopane/sterane ratio, which seems not to be the case. However, if the endosymbionts were photoautotrophs like coral zooxanthellae, then their potential biosignatures may depend both on their nature and their abundance. Nevertheless, there is no indication from the biomarkers that *Dickinsonia* housed any kind of endosymbiont. Thus, it is most likely that *Dickinsonia* was a phagocytic ingester of prokaryotes and/or microscopic eukaryotes. If Bobrovskiy *et al.* (2020) are correct in their supposition that eukaryotes were the principal food source, then there are two possible supply pathways: planktonic green algae (Bobrovskiy *et al.* 2020) or benthic members of the meiofauna (Deline *et al.* 2018). How either kinds of organisms could be captured and taken in remains a mystery, but placozoan-like grazing on cyanobacterial mats (Sperling & Vinther, 2010) is equally difficult to envisage. To paraphrase Ellis Yochelson (1928–2006), Quo vadis *Dickinsonia*? On the other hand, Ivantsov & Zakrevskaya (2021b) have made a compelling case for planktotrophy and dorsal ciliary tract feeding in the Trilobozoa.

4.d. Could Ediacaran animals move?

A number of resting and movement traces have been attributed to Ediacaran organisms, but two kinds stand out: (1) overlapping resting traces attributed to movements made by individuals of *Dickinsonia* and *Yorgia* (Ivantsov, 1999; (2) scratch marks (*Kimberichnus* Ivantsov, 2013) that are frequently associated with body fossils of *Kimberella* (Wade, 1972b (Ivantsov, 2009, 2013; Gehling *et al.* 2014). For the purpose of this discussion, I assume that both were produced by the organisms during life rather than being the result of environment-driven transport (McIlroy *et al.* 2009), given their taxonomic specificity. So the question is, was this by ciliary gliding (Martin, 1978), amoeboid crawling (Bond & Harris, 1988; Arendt *et al.* 2015; Brunet & King, 2017) or muscular motion, the three energetic methods of movement available to animals? My money is on the first for *Dickinsonia* and *Yorgia*; for *Kimberichnus*, it is more important to decide whether it was all or only some of the animal that was moving. We can say ‘animal’ more comfortably here because motility is one feature that helps to distinguish animals from all other kinds of megascopic life.

Living multicellular choanoflagellates use the muscle protein myosin for movement (Brunet *et al.* 2019). They can invert a cup-shaped ‘colony’ so that the collar cells can face inwards or outwards. And some sponges can move, albeit slowly and inefficiently (Bond & Harris, 1988). If we think of life at the turn of the eon, being able to move was about as valuable a thing as anyone could imagine. Hyoliths, for example, seem to have evolved oar-like calcareous poles (helens) in order to be able to move a little (Runnegar *et al.* 1975; Martí Mus *et al.* 2014). Moving first by cellular processes, especially ciliary gliding, could have been the first step towards animal mobility.

If the *Dickinsonia* and *Yorgia* footprints are locomotion trails, then it is striking that they are unidirectional in a way that conforms to the traditionally assumed anterior–posterior axis of the body (Glaessner & Wade, 1966; Runnegar, 1982). What was the motive of this unidirectional motion – best shown on the 1T-NA surface at Nilpena as documented by Evans *et al.* (2019) – and how was it specified? It may be useful to think of minimal requirements such as navigation by solar tracking and photoreceptors no more complicated than flatworm eyespots. Even slime moulds display some phototaxis (Bonner & Lamont, 2005).

Although passive transport by bottom currents seems unlikely to have produced the serial footprints of *Dickinsonia* and *Yorgia*, there is at least one good example of probable passive transport, the holotype of *D. tenuis*, which overlies the sand-filled stem of a felled *Arborea* that retains both the circular holdfast and the lower branches of the frond (Glaessner & Wade, 1966, pl. 103, fig. 1).

4.e. What was the composition of the tough organic integument?

There are two approaches to this question, phylogenetic and taphonomic. If, for example, *Dickinsonia* was an annelid then its body wall should have been constructed from a chitinous and collagenous cuticle strengthened by circular and longitudinal muscles and connective tissue. Similarly, if *Charnia* and *Charniodiscus* were coelenterates, their body walls should have been composed of collagenous mesogloea sandwiched between inner and outer layers of epithelial cells. Alternatively, the preservation of the fossils themselves might suggest that they were made from a leathery (collagenous) material, plant-like biopolymers or something else.

With characteristic perceptiveness, Seilacher (1989) described the vendozoan integument as flexible but also malleable, watertight yet permeable, and cuticular but expandable during growth. Noting that the integument of *Ernietta* was both flexible and elastic, Dzik (1999) concluded that it must have been composed of collagen and served, like the myosepta of cephalochordates, to enclose the muscle blocks of a hydrostatic skeleton. Although collagenous macromolecular structures are sometimes preserved, most notably in graptolite periderm (Runnegar, 1986), they are not chemically proteins, which disappear swiftly unless encased in mineral skeletons. So, although we know a good deal about the biochemical components of the membranes of the cells of *Dickinsonia* (Bobrovskiy *et al.* 2018), there is as yet no ultrastructural or chemical evidence for the nature of the body wall of any Ediacaran soft-bodied organism.

5. Some comments on key taxa: *Pteridinium*, *Ernietta*, *Dickinsonia*, *Arborea*, *Kimberella*

5.a. *Pteridinium* *Gürich*, 1933

Pteridinium is an exemplar of the Nama association, in that it is a foliated organism formed of three quilted vanes and is commonly preserved in three dimensions within sandstone beds (Richter, 1955; Glaessner & Wade, 1966; Pflug, 1970; Jenkins, 1992; Narbonne *et al.* 1997; Dzik, 1999; Meyer *et al.* 2014b). It has been reconstructed in several different ways but its affinities and mode of life remain controversial. One prominent hypothesis – that *Pteridinium* was canoe-shaped and lived partly or wholly within the sediment in which it is found (Pflug, 1970; Grazhdankin & Seilacher, 2002) – is almost certainly incorrect. It is most likely that

Pteridinium was the principal and perhaps propagative part of an upright organism that is nearly always preserved as a transported, deformed and pliable shroud. Its early life stage and attachment structure, if any, may not have been identified. Given its threefold symmetry, it is even possible that *Pteridinium* is the dispersed frond of one or more coeval trilobozoan discs, such as *Tribrachidium* Glaessner *in* Glaessner & Daily, 1959 or *Rugoconites* Glaessner & Wade, 1966.

Gürich (1933) had only two inferior specimens of *Pteridinium* to work with and did not discover the third vane. Richter (1955) had much better material but came to the strange conclusion that specimens with three vanes were caused by the close packing of left- and right-handed two-vaned individuals, which were twinned like crystals during growth from the sea floor. Nevertheless, Richter did have a clear view of the mode of life and taphonomy of *Pteridinium*, imagining it to have been rooted in unconsolidated sediment, grown gregariously and, like kelp forests, flexed with the currents and the tides. His choice of a gorgoniid octocoral – the angular sea whip, *Pterogorgia anceps* – as the closest living analogue was based on its commonly Y-shaped cross-section plus the fact that gorgoniids are readily rooted within soft substrates whereas kelps normally require rocky or stony bottoms. Richter also concluded that the fronds of *Pteridinium* were tall and tapered slowly from a maximum measured width of 16 cm. The longest vane available to him was 37 cm, comparable to the longest incomplete individual (41.5 cm) reported by Grazhdankin & Seilacher (2002), so fronds of *Pteridinium simplex* could have been a sizeable fraction of a metre in height. However, very few specimens of *P. simplex* show a close approach to the end of a frond (Fig. 9), and as no termination has been reported, it is possible that growth continued for more than a metre.

The unipolarity of *Pteridinium* was confirmed by the discovery of additional species, most notably *P. carolinaense*, famously first described as a trilobite (St Jean, 1973). However, Richter had deduced it from the curvature of the vane quilts, which are convex in the apical direction. The 3D shape of the termination has been less well understood, as two end-member hypotheses illustrate. In the ‘canoe’ model for *Pteridinium* (Pflug, 1970; Buss & Seilacher, 1994; Crimes & Fedonkin, 1996; Grazhdankin & Seilacher, 2002; Meyer *et al.* 2014a; Droser *et al.* 2017), two of the vanes form the prows and hull of a canoe-shaped organism that was at least partially buried in the sediment during life; the third vane had the form of a retracted keel running down the length of the canoe. Even more strikingly, Grazhdankin and Seilacher believed that one end of the canoe could reverse direction during extensional growth and that the keel vane of the older, deeper part of the organism could become one of the hull vanes of the younger, shallower section (Grazhdankin & Seilacher, 2002, text-fig. 5C). Additional speculations, not considered here, were interpenetrative growth, where one individual might grow through a pre-existing one without disrupting either, and growth solely within the pore space of the enclosing sand (Crimes & Fedonkin, 1996).

The alternative end-member model for vane orientation is best illustrated by reconstructions of *Swartpuntia germsi* (Narbonne *et al.* 1997). Although originally described as having four or more vanes, *Swartpuntia* probably had only three (Narbonne, 1998, fig. 1B) and possibly no stalk or holdfast. As such, it is close to *Pteridinium*, perhaps even congeneric, if you happen to be a lumpner rather than a splitter. Because *Swartpuntia* has always been considered to be an upright organism, its vanes are thought to have been flat and equally spaced radially. The same configuration may be true for *Pteridinium*, as Jenkins (1992) surmised.

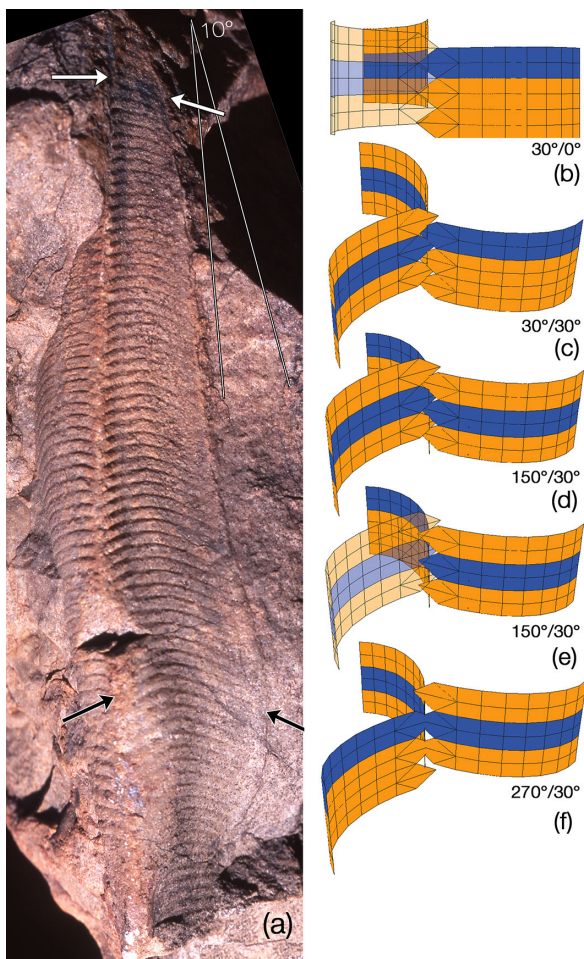


Fig. 9. Geometry of *Pteridinium simplex*. (a) Exceptional specimen showing tapered approach to the distal end of the organism (top) and measured widths of the right-hand vane between upper arrows (13 mm) and lower arrows (24 mm); unnumbered specimen in the private collection of Wilfried Erni, Plateau Farm, Aus district, Namibia photographed on site in 1996; previously illustrated by Laffamme & Narbonne (2008, fig. 5.5). (b–f) Differently rotated views of part of a model for the orientation and interdigitation of the three vanes. Vanes are modelled as flat curved surfaces set at 120° to each other. Each set of vanes is offset by one module in two of the three intersections (c), (d), (e), but the ends of the modules are opposite each other in the third position (b), (f). Angles are rotations about the axis of the model and tilt with respect to the model. One set of modules is shown in blue for clarity.

The mode of articulation of the quilts of the vanes has also been interpreted in different ways. Ideally, three equally spaced, equal size vanes would be opposite each other across the axis or be offset from each other by an equal amount. In theory, a one third offset of each quilt with respect to the quilts of the adjacent vane, taken in order, would result in [123] or [132] glide symmetries, where 1, 2 and 3 denote the individual vanes (Tojo *et al.* 2007). This was the design adopted by Grazhdankin & Seilacher (2002, text-fig. 6H) for their canoe keel. However, Pflug (1970), Jenkins (1992) and others have inferred more elaborate architectures, which result in some pairs of vanes being articulated in an elementary zig-zag fashion (Tojo *et al.* 2007, fig. 4A2–A3). In other orientations, there may also be a chain of matrix-filled beads between the proximal edges of the two visible vanes (Grazhdankin & Seilacher, 2002, text-fig. 6F; Pflug, 1970, text-fig. 3E, pl. 21, fig. 2, text-fig. 8D, pl. 22, fig. 1). These are the structures that led Jenkins (1992) erroneously to reconstruct *Pteridinium* with two layers of tubular quilts per vane, but they are readily explained as ends of quilts of

the third vane, which are visible through apertures in the seam (Figs 9, 10). Thus, *Pteridinium* did not have perfect three-fold symmetry; rather, it had a best approximation to three-fold symmetry, given the constructional constraints for packing tubular quilts in three dimensions. Achieving the ideal geometry of perfect symmetry (Tojo *et al.* 2007) was probably beyond the developmental capabilities of this organism.

5.b. *Ernietta Pflug, 1966*

Ernietta (Fig. 3) was a bag-shaped organism constructed from the same kind of modules as *Pteridinium* (Pflug, 1970, 1972b; Jenkins *et al.* 1981; Dzik, 1999; Elliott *et al.* 2016; Ivantsov *et al.* 2016) and probably *Phyllozoon* (Gehling & Runnegar, 2021). Reconstructions by Jenkins (in Jenkins *et al.* 1981) and Ivantsov *et al.* (2019c) are remarkably similar and perhaps both incorrect in the same two interconnected ways. It is unequivocal that some specimens from Aar show evidence for walls made of more than one layer of tubular modules (Jenkins *et al.* 1981; Elliott *et al.* 2016) and that many specimens have a constriction at their waist, but I would argue that these two phenomena may be site-specific and causally connected. The constrictions may be due to injury and truncation during a storm surge (Jenkins, 1985, fig. 1) and the duplicate walls to secondary regrowth of the truncated parts. An analogous situation is seen in cohorts of *Dickinsonia menneri* from the White Sea (Ivantsov *et al.* 2020). If true, this would make *Ernietta plateauensis* a far simpler organism than previously thought and one that was capable of vegetative regrowth. All known specimens from Nevada show no trace of these features (Smith *et al.* 2017). Furthermore, *Ernietta* from Nevada (Smith *et al.* 2017, fig. 3d; Hall *et al.* 2020, fig. 1b) and at least one specimen from Namibia (Narbonne, 2004a, fig. 4b) have modules that terminate distally in pointed tips (Fig. 3a) well separated by open spaces, rather different from the situation seen in the two reconstructions. This is an indication that the modules were independent units that merged during growth rather than subdivisions of the whole (Gehling & Runnegar, 2021). Seilacher (1992) had stipulated the opposite when characterizing the Vendobionta.

5.c. *Dickinsonia Sprigg, 1947*

The type species, *Dickinsonia costata* Sprigg, 1947, is an iconic Ediacaran fossil, a core member of the Vendozoa (Seilacher, 1989) and a candidate bilaterian animal (Gold *et al.* 2015). Seen in plan view as it is presumed to have lived on the sea floor, *D. costata* is almost circular (Fig. 4b), bilaterally symmetrical and differentiated into a proximal or ‘anterior’ end with a single undivided module lying across the midline and a distal or ‘posterior’ end, from which growth proceeds (Ivantsov *et al.* 2020). Suggestions that growth might have proceeded in the opposite direction (Hoekzema *et al.* 2017; Dunn *et al.* 2018) were falsified recently by the discovery of a cohort of individuals of *D. cf. menneri* Keller, 1976 in Keller & Fedonkin, 1976, several of which had regenerated the ‘posterior’ end of the body by growing new modules following non-lethal loss (Fig. 4a; Ivantsov *et al.* 2020). However, closer inspection of the outline of *D. costata* reveals that it may be better approximated by the curve known as a cardioid rather than a circle or ellipse, a shape that has not been replicated in any of the proposed growth models. It is also a propensity taken to extremes by Andiva Fedonkin, 2002, where the site of ‘terminal addition’ (Gold *et al.* 2015) has moved so far forward as to be in the anterior half of the body (Ivantsov, 2007, pl. 1, fig. 6).

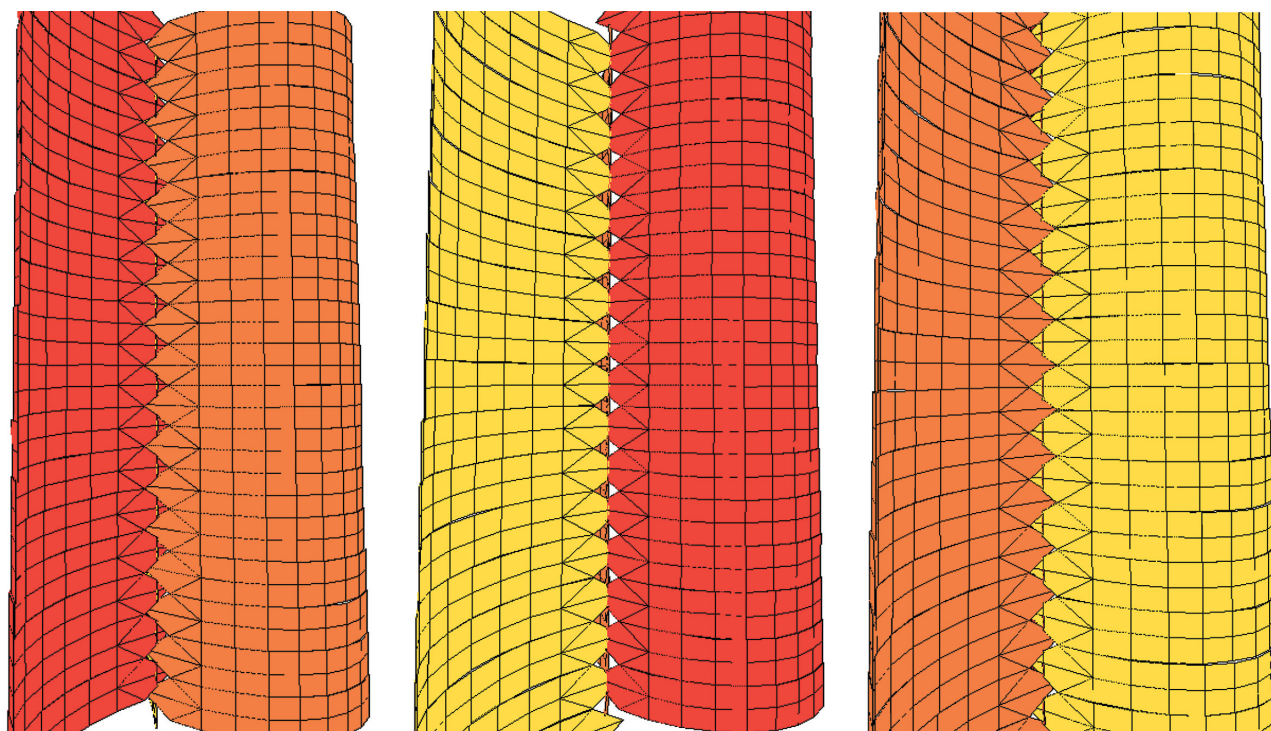


Fig. 10. Toy 3D model of part of a frond of *Pteridinium simplex* rotated through 120° and 240° to show views of the intersections between adjacent pairs of vanes. Note that in the left and right images the sutures between modules are offset in a zig-zag fashion, whereas in the middle image the modules of adjacent vanes are opposite one another and there is a series of rhomboidal gaps along the axis, as found in a number of fossils.

As is well known, the body of *Dickinsonia costata* was constructed from segments, isomers, units or modules, which appeared at an unresolvable size at the ‘posterior’ end and continued to grow and change shape during the life of the animal (Runnegar, 1982; Evans *et al.* 2017). This alone is a feature of animals rather than plants, kelps or fungi. The modules are defined by raised ridges on the upper surface of specimens preserved in the typical way (concave hyporelief), both in South Australia and Russia, and by grooves in the impressions of lower surfaces (Fig. 4b, c; Seilacher, 1989, fig. 5). In large specimens, such as the frequently illustrated *D. costata* from Brachina Gorge (Wade, 1972a, pl. 5, figs 1, 2; Runnegar, 1982, figs 4, 5; Seilacher, 1989, figs 3, 5; Retallack, 2007, fig. 1A; Budd & Jensen, 2017, fig. 4E) or the 1 m sized *D. rex* Jenkins, 1992 (Gehling *et al.* 2005, fig. 4), the peripheral ends of the ridges are expanded and imbricated in ways that imply that the module walls were stiff like the ‘struts of a glider plane wing’ (Fig. 4a; Seilacher, 1989, p. 236).

This brings us to the contentious matter of whether or not *Dickinsonia* exhibits glide symmetry (Fig. 4a, b). The Australian position is ‘no’, based on a large cohort of small individuals of *D. costata* from a single surface in Crisp Gorge, central Flinders Ranges (Gold *et al.* 2015; Reid *et al.* 2017) as well as numerous specimens from other localities. In contrast, Russian workers identify glide symmetry in all species of *Dickinsonia*, including *D. menneri* and *D. costata* (Ivantsov, 2007; Ivantsov *et al.* 2020). To some extent, this difference of opinion is hypothesis driven, but it is clear that other members of the same ‘orphan plesion’, the Proarticulata, clearly show this property. Perhaps the most convincing example is the specimen of *Andiva ivantsovi* Fedonkin, 2002 illustrated by Dunn *et al.* (2018, fig. 4), where the insertion of new modules is shown to have occurred alternately

on left and right sides of the body. It is time for Australians to acknowledge that proarticulate glide symmetry is a widespread feature of this putative clade and for Russians to admit that some members of the group do not display it.

Much has been written about the internal anatomy of *Dickinsonia*, starting with Glaessner and Wade’s discovery of the casts of intestinal caeca on a single specimen of *D. costata* from Ediacara (Glaessner & Wade, 1966, pl. 101, fig. 4). As confirmation from other specimens failed to materialize, this observation was either disregarded (Runnegar, 1982) or embellished (Jenkins, 1992, fig. 13). Nevertheless, the elevated axial ridge or pair of ridges that are found on many Australian and Russian specimens have been interpreted as evidence for a sediment-filled gut (Wade, 1972a; Runnegar, 1982; Ivantsov, 2004), which terminated at the posterior end of the ‘0 module’ (Fig. 4a; Runnegar, 1982, fig. 1C, F; Gehling *et al.* 2005, fig. 4a; Sperling & Vinther, 2010, fig. 1A; Gold *et al.* 2015, fig. 1D; Evans *et al.* 2017, fig. 3b; Hoekzema *et al.* 2017, fig. 1). According to the proarticulate hypothesis, the ‘gut’ consisted of two parallel tubes on either side of an axial partition against which the left and right half modules or ‘isomeres’ abutted (Ivantsov, 2011, fig. 6). The prominence and yet narrowness of this feature in some specimens of *Dickinsonia* (Gehling *et al.* 2005, fig. 4; Ivantsov, 2007, pl. 1, fig. 1), *Yorgia* (Ivantsov, 1999, pl. 1, fig. 4; Evans *et al.* 2019, fig. 12d) and *Andiva* (Ivantsov, 2007, pl. 1, fig. 6) make the gut interpretation improbable; a constructional or some other function seems more likely. Particularly telling is the remarkable imprint (*Epibaion axiferus*) of the putative lower surface of *Dickinsonia* cf. *tenuis* (Ivantsov & Malakhovskaya, 2002, pl. 2, fig. 3; Ivantsov, 2011, pl. 2, fig. 1; Ivantsov, 2013, pl. 1, fig. 1), which shows the left and right side modules joined to a well-defined axis. It is hard to imagine how an internal organ could be expressed so crisply

externally, although it may have been in a similarly axial position. However, Ivantsov's (2011) concept of a median septum with longitudinal 'feeding channels' on either side makes more sense for the numerous specimens that have elevated ridges on either side of a depressed midline, as is typical of *Dickinsonia lissa* Wade, 1972a (Runnegar, 1982, fig. 1A-B; Ivantsov, 2007, pl. 1, fig. 1). Perhaps the axial ridge is nothing more than a topographic high produced during burial by fluid flow from the modules; its prominence in *D. lissa* may be owing to the fact that the modules are exceptionally narrow and thus constrained all body fluids to move in an axial direction.

Three discoveries made at the White Sea have allowed more elaborate reconstructions to be made of *Dickinsonia*'s soft parts. First, several specimens of *Dickinsonia* cf. *lissa* with complexly corrugated surfaces were discovered at Zimmie Gory (Dzik & Ivantsov, 2002). The corrugations, which radiate and branch towards the 'anterior' direction, were thought to overlie a straight gut and its diverticula as best shown in a cutaway perspective view drawn by Dzik (2003, fig. 6). However, it is notable that Dzik's drawings show no trace of glide symmetry in the internal organs, an anomaly corrected by Ivantsov (2004, fig. 6); the specimens themselves are ambiguous in this respect. Furthermore, although the corrugations superficially resemble the isomers of other White Sea proarticulates such as *Vendia rachiata* Ivantsov, 2004, it was necessary for Budd & Jensen (2017, fig. 4) to rotate one of the corrugated specimens of *D. cf. lissa* through 180° to make the visual comparison meaningful. The only other Ediacaran fossil with comparable corrugations is the holotype of *Chondroplon bilobatum*, which comes from a mass flow sandstone at Ediacara, and thus is preserved in the Nama manner (Wade, 1971). Hofmann (1988) reinterpreted *Chondroplon* as a deformed *Dickinsonia*, a view that was adopted by Dzik & Ivantsov (2002). However, it is difficult to exclude the possibility that the corrugations in both taxa are taphonomic effects caused by contractions parallel to the trend of the modules rather than crinkles above incompressible organs (Budd & Jensen, 2017).

The two other discoveries are feathery and beaded structures within modules of *Yorgia* and *Dickinsonia* (Ivantsov, 2013, pl. 1, figs 3, 4) and a remarkable incomplete specimen of *Dickinsonia* cf. *tenuis*, in which the tubular modules were apparently filled with fine sediment (Ivantsov, 2011, pl. 1, fig. 3). Modules of undescribed specimens of *D. rex* Jenkins, 1992 from Nilpena were also filled in this way (J. G. Gehling, pers. comm.). Taken together, these observations tell us little about the internal anatomy of *Dickinsonia* and the other proarticulates. At best, Seilacher's characterization of them as fluid-filled 'pneus' may serve as the current null hypothesis.

5.d. *Arborea* Glaessner & Wade, 1966

Ford's chimera of *Charnia* and *Charniodiscus* (Fig. 2) serves as a graphical abstract for the Arboreomorpha and Rangeomorpha, two putatively monophyletic clades that may together constitute a monophyletic or paraphyletic group. The tortuous taxonomic trajectory of *Arborea* reminds us of the obvious similarities yet important differences between the arboreomorphs and rangeomorphs, which have been carefully and thoroughly explored by Canadian and British teams led by Guy Narbonne and Martin Brasier (1947–2014), respectively, over the past several decades.

The first collection of fronds from Ediacara included several slabs of *Arborea* and one of *Charnia*. All were referred to Gürich's genus *Rangea*, but in an addendum added after Ford's

(1958) article was published, Glaessner noted that one was a *Charnia* not a *Rangea* (Glaessner & Daily, 1959). By 1960, all of the Ediacaran fronds had become *Charnia* (Fig. 2; Glaessner, 1962), but in 1966 *Charnia* had gone and all of the fronds were now split between two new species of *Rangea* and the type species of the new genus, *Arborea* (Glaessner & Wade, 1966). The original example of *Charnia* was rescued by Germs (Germs, 1973), who named it *Glaessnerina*, now a junior synonym of *Charnia*. Then in 1978, Jenkins & Gehling (1978) synonymized *Arborea* with *Charniodiscus* and she remained in limbo until resurrected from obscurity (Laflamme *et al.* 2018; Dunn *et al.* 2019; Wang *et al.* 2020). All of this equivocation argues for a biological relationship between *Charnia* and *Arborea* that is significant at the scale of this review.

The anatomy of *Charnia masoni* and its relatives have been beautifully revealed by numerous studies of occurrences in Avalonian England and Newfoundland (Narbonne, 2004b; Antcliffe & Brasier, 2006; Gehling & Narbonne, 2007; Laflamme *et al.* 2007, 2012; Hofmann *et al.* 2008; Narbonne *et al.* 2009; Brasier *et al.* 2012; McIlroy *et al.* 2020). Rangeomorphs are frondose taxa that maximized surface area via fractal growth (Fig. 8). The most obvious links to the Arboreomorpha are their similar body forms and discoidal holdfasts, at least in some members of each group. I treat them as a paraphyletic grade for the sake of simplicity (Fig. 12); cladistic analyses have recovered the Erniettomorpha as sister of the Rangeomorpha (Decocchi *et al.* 2017; Hoyal Cuthill & Han, 2018), and it is plausible to refer all three groups to Pflug's Petalonamae. However, major differences in construction of the three groups, summarized in the first five characters of Decocchi *et al.*'s data matrix (modular or not, branching or not, tubular modules or not, fractal construction or not, differentiated elements or not), also permit the following relationship: (Erniettomorpha (Arboreomorpha, Rangeomorpha)).

5.e. *Kimberella* Wade, 1972b

When Glaessner & Wade (1966) first described *Kimberella* (as *Kimberia quadrata*), Sprigg's jellyfish hypothesis was state of the art, and so they doubled the visible bilateral symmetry on the assumption that they were looking at a crushed hydrozoan or cubozoan medusa. Wade (1972b) extended this way of thinking but was unwilling to refer *Kimberella* to either the Hydrozoa or the Cubozoa, preferring to regard it as something like a stem member of one or both of these groups (Glaessner, 1984, fig. 3.2). However, Jenkins (1984) confidently considered *Kimberella* to be ancestral to the living box jellyfish and even speculated that cubozoans refined and perfected their potent venom over an eon of evolution. One reason this jellyfish hypothesis seemed to work so well is that almost every Australian specimen of *Kimberella* has a well-rounded and clearly formed end (the bell) and fades out at the other end into what may be thought of as tentacles.

The breakthrough with *Kimberella* came with the discovery of much better material in Russia and its analysis by Fedonkin & Waggoner (1997). Unfortunately, although the bilateral symmetry seems clear, there was and still is no other character that could identify *Kimberella* as a mollusc or even a bilaterian animal. However, sets of paired scratch marks, found in fan-shaped arrays on bed bases and interpreted as possible arthropod scratch marks, had been previously illustrated by Gehling (1991, pl. 6, fig. 3) and their producer adventurously reconstructed by Jenkins (1992, fig. 10). The association of these trace fossils, now known as *Kimberichnus teruzzi* (Ivantsov, 2013; Gehling *et al.* 2014), has

firmed up the idea that *Kimberella* was a bilaterian metazoan (Fedonkin *et al.* 2007; Ivantsov, 2009, 2013).

There are, however, some difficulties with attributing the traces to *Kimberella*. The body fossils obviously pre-date the deposition of the event bed that buried them, but the time of formation of the traces is more uncertain. Given their similarity to *Monomorphichnus* Crimes, 1970 (Jenkins, 1992, 1995) – one of Seilacher's (2007) trilobite 'deep undertraces'—they could have been made after the storm sand was deposited. That could explain how *Kimberichnus* was superimposed on an *Aspidella* holdfast (Ivantsov *et al.* 2020, fig. 1) and a *Phyllozoon* frond (Gehling & Runnegar, 2021, fig. S3a); undertraces are constructed with the soft sand in place. The alternative hypothesis, that the traces were made by mining an exposed mat surface, requires the paired scratches to remain open for extended periods of time (e.g. Gehling *et al.* 2014, fig. 6), a problem perhaps solved by Budd & Jensen (2017, p. 458), who concluded that the sharpness of the scratches shows 'that they were not formed in the mat but rather in the sediment underlying the mat.' However, this is unlikely to be true for the *Kimberichnus* found in Bathub Gorge, South Australia, where the underlying bed has a coarse sugary top that contrasts with the fine base of the overlying event bed (Gehling & Runnegar, 2021). The production of *Kimberichnus* needs additional investigation.

The most striking feature of the anatomy of *Kimberella* is the so-called 'crenellated zone', which encircles most of the body and generally lies inboard of a well-defined rim (Fedonkin & Waggoner, 1997). The preservation of this feature varies greatly from non-existent to ladder-like in expanded specimens. It has been reconstructed as a ruff-like extensible mantle (Fedonkin & Waggoner, 1997, fig. 2b; Fedonkin *et al.* 2007, fig. 23d), as the scalloped zone of a dorsal carapace (Ivantsov, 2013, 2017) and in the box jellyfish phase, as pouched gonads attached to radial canals (Wade, 1972b, text-fig. 6; Jenkins, 1984, text-fig. 2). The evidence for this crenellated zone being suspended above the sides of the body is slight and in many specimens, small and large, the crenellations extend to the rim. However, in those cases they look more like regularly arranged anticlinal ridges than ruff-like folds. Similar angular ridges are seen in specimens of *Temnoxa molliuscula* and *Keretsa brutoni* (Ivantsov, 2017; Ivantsov & Zakrevskaya, 2021c), which like *Kimberella*, have a rounded larger terminus and a tent-like shape following compaction. Australian specimens of *Keretsa* and *Kimberella* are even more similar in these respects (Gehling, 2005, fig. 12K; Gehling *et al.* 2005, fig. 12).

There are many other well-characterized aspects of the anatomy of *Kimberella*, but it is the flat and probably muscular base that most obviously suggests an affinity with the Mollusca. However, extended specimens that are connected to fan-shaped arrays of *Kimberichnus* plausibly made by them, suggest alternative possibilities (Ivantsov, 2009; Gehling *et al.* 2014), one of which might be an animal of cnidarian grade. It is possible to regard *Kimberella* as some kind of foraging anemone, anchored by an aboral pedal disc and collecting food with a cuticularized oral apparatus that acted more like a rake than a pair of claws (Ivantsov, 2009). It may not have moved around much, if at all, operating more like a strip-mining dragline than a mechanical excavator (Gehling *et al.* 2014, fig. 9).

6. Speculative discussion

6.a. Introduction

Despite all of the research that has been accomplished over the past three quarters of a century and the dedicated contributions of

many talented palaeobiologists, the presumed affinities of Ediacaran organisms have, on average, hovered continuously around the coelenterate grade, although there has been significant stemward slippage in recent years (Table 1). The only really positive assignments, such as Glaessner's Pennatulacea hypothesis, have been falsified, and the current approach of seeking ever more detailed and quantifiable knowledge (Laflamme *et al.* 2004; Evans *et al.* 2017; Hoekzema *et al.* 2017; Hoyol Cuthill & Han, 2018) has not, as yet, led to startling outcomes. Perhaps the time is ripe for some speculative, even outlandish thinking. It may also be useful to review briefly previous ways of dealing with problematical fossils.

6.b. Prior Problematica

Palaeontologists have long been perplexed by problematical fossils, particularly by those with no obvious living counterparts (Bengtson, 1986). Famous examples include rudist bivalves (Skelton, 2018), graptolites (Mitchell *et al.* 2013), archaeocyaths (Rowland, 2001) and the phosphatic microfossil *Microdictyon*, which as the authors who named it noted, is 'shaped like a little net' (Bengtson *et al.* 1986). Of these conundrums, rudists were solved first by S. P. Woodward, author of *A Manual of the Mollusca* (1851–1854), in a remarkably advanced article published even before brachiopods were removed from the phylum. Woodward's words resonate today despite his firm belief in Divine creation rather than Darwinian transmutation: 'In searching out the affinities of a problematic fossil shell, it is desirable to inquire, first, whether any similar, but less abnormal, forms occur in the same stratum with it, or in formations immediately older or newer. . . . We think it may be shown, that, by a complete series of cognate forms, the Cretaceous *Hippurites* are connected with the Oolitic *Dicerata* and the Tertiary *Chamae*.' (Woodward, 1855, p. 46). Thus, these strange coral-like bivalves (Fig. 11b) were confidently identified as a major extinct clade of the Bivalvia by the mid-nineteenth century (Skelton, 2018; Rineau *et al.* 2020).

Clarification of the affinities of graptolites followed another path. Roman Kozłowski's pre-Second World War discovery of extractable, three-dimensionally preserved colonies in Polish Ordovician limestones revealed the fine structure of the periderm to be formed of 'half rings' as in living pterobranchs (Fig. 11a; Kozłowski, 1947). The hemichordate hypothesis received a second boost when Towe & Urbanek (1972) provided ultrastructural evidence that the graptolite periderm was composed of collagen rather than cellulose or chitin (Runnegar, 1986), and has been accepted ever since. In this case, it was new information from both the fossils and their living relatives that turned the tide.

Archaeocyaths (Fig. 11d) are another previously problematical group that was passed around phylogenetically speaking until the emergence of two mid-twentieth century hypotheses: an extinct phylum, the Archaeocyatha (Hill, 1964) or kingdom, the Archaeata (Zuhuravleva & Myagkova, 1972); or an extinct sponge clade and grade. The second alternative is now mainstream; its acceptance required the SCUBA-enabled discovery of living aspiculate sclerosponges as analogues for archaeocyaths (Vacelet, 1985; Kruse, 1990; Rowland, 2001).

In contrast, *Microdictyon* (Fig. 11c) was one of the many small shelly fossils that fell out of early Cambrian carbonates dissolved slowly and laboriously in acetic acid (Bengtson *et al.* 1986). Speculations about its affinity and function were wide ranging and numerous, but the solution seemed absurd when it suddenly appeared. Stefan Bengtson and I were sitting together in a meeting at UCLA when he opened a letter from China that contained a

Table 1. Chronology of taxonomic assignments to core members of the Ediacara biota. Note the stemward movement as time progresses. Cnidaria highlighted in grey

Date	Taxon/Author	<i>Arborea, Charniodiscus</i>	<i>Ediacaria, Cyclomedusa</i>	<i>Charnia, Rangea</i>	<i>Pteridinium, Ernietta</i>	<i>Dickinsonia, Yorgia</i>	<i>Kimberella, Keretsa</i>
1946–1949	Sprigg	algae	Cnidaria: Medusozoa	?		Cnidaria: Medusozoa	
1955	Richter			?	Cnidaria: Anthozoa		
1955	Harrington & Moore					Cnidaria: Medusozoa	
1957	Caster		Cnidaria: Medusozoa				
1957–1961	Glaessner	Cnidaria: Anthozoa	Cnidaria: Medusozoa	Cnidaria: Anthozoa		Annelida: Sedentaria	
1958–1963	Ford	algae	algae	algae	algae		
1966–1972	Pflug	stem Metazoa?		stem Metazoa?	stem Metazoa?		
1966–1972	Glaessner & Wade	Cnidaria: Anthozoa	Cnidaria: Medusozoa	Cnidaria: Anthozoa	Cnidaria: Anthozoa	Annelida: Sedentaria	Cnidaria: Medusozoa
1978	Jenkins & Gehling	Cnidaria: Anthozoa					
1983–1992	Seilacher	stem Metazoa	stem Metazoa	stem Metazoa	stem Metazoa	stem Metazoa	
1981–1987	Fedonkin	TG Metazoa	Cnidaria: Cyclozoa	TG Metazoa	TG Metazoa	stem Protostomia	Cnidaria: Medusozoa
1984–1990	Jenkins	Cnidaria: Anthozoa	Cnidaria: Medusozoa	Cnidaria: Anthozoa	Cnidaria: Anthozoa	Annelida: Sedentaria	Cnidaria: Medusozoa
1992	Valentine					stem Cnidaria?	
1991–1992	Runnegar	Cnidaria: Anthozoa	Cnidaria: Medusozoa	Cnidaria: Anthozoa		Annelida?	
1992+	Seilacher	TSAR: Alveolata	TSAR: Alveolata	TSAR: Alveolata	TSAR: Alveolata	TSAR: Alveolata	Mollusca: Gastropoda
1994	Buss & Seilacher	stem Cnidaria	stem Cnidaria	stem Cnidaria	stem Cnidaria	stem Cnidaria	
1994+	Retallack		lichenized Fungi			lichenized Fungi	
1997	Fedonkin & Waggoner						stem Protostomia
2006	Zhang & Reitner					Ctenophora	
2009+	Ivantsov	TG Metazoa	TG Metazoa	TG Metazoa	TG Metazoa	stem Protostomia	crown Protostomia
2017	Budd & Jensen	stem Eumetazoa		stem Metazoa		stem Eumetazoa	stem Bilateria
2017	Cavalier-Smith	stem Metazoa	stem Metazoa	stem Metazoa	stem Metazoa	stem Metazoa	
2017	Dufour & McIlroy	stem Eumetazoa	stem Eumetazoa	stem Eumetazoa	stem Eumetazoa	stem Eumetazoa	
2018	Hoyal Cuthill & Han	stem Eumetazoa	stem Eumetazoa	stem Eumetazoa	stem Eumetazoa	stem Eumetazoa	
2018	Dunn, Liu & Donoghue			stem Eumetazoa			stem Bilateria
2021	Evans, Droser & Erwin					stem Bilateria	crown Bilateria
2021	This review	stem Eumetazoa	stem Eumetazoa	stem Eumetazoa	stem Eumetazoa	stem Bilateria?	stem Coelenterata?

TG - total group; TSAR - Telenemia + Stramenopila + Alveolata + Rhizaria.

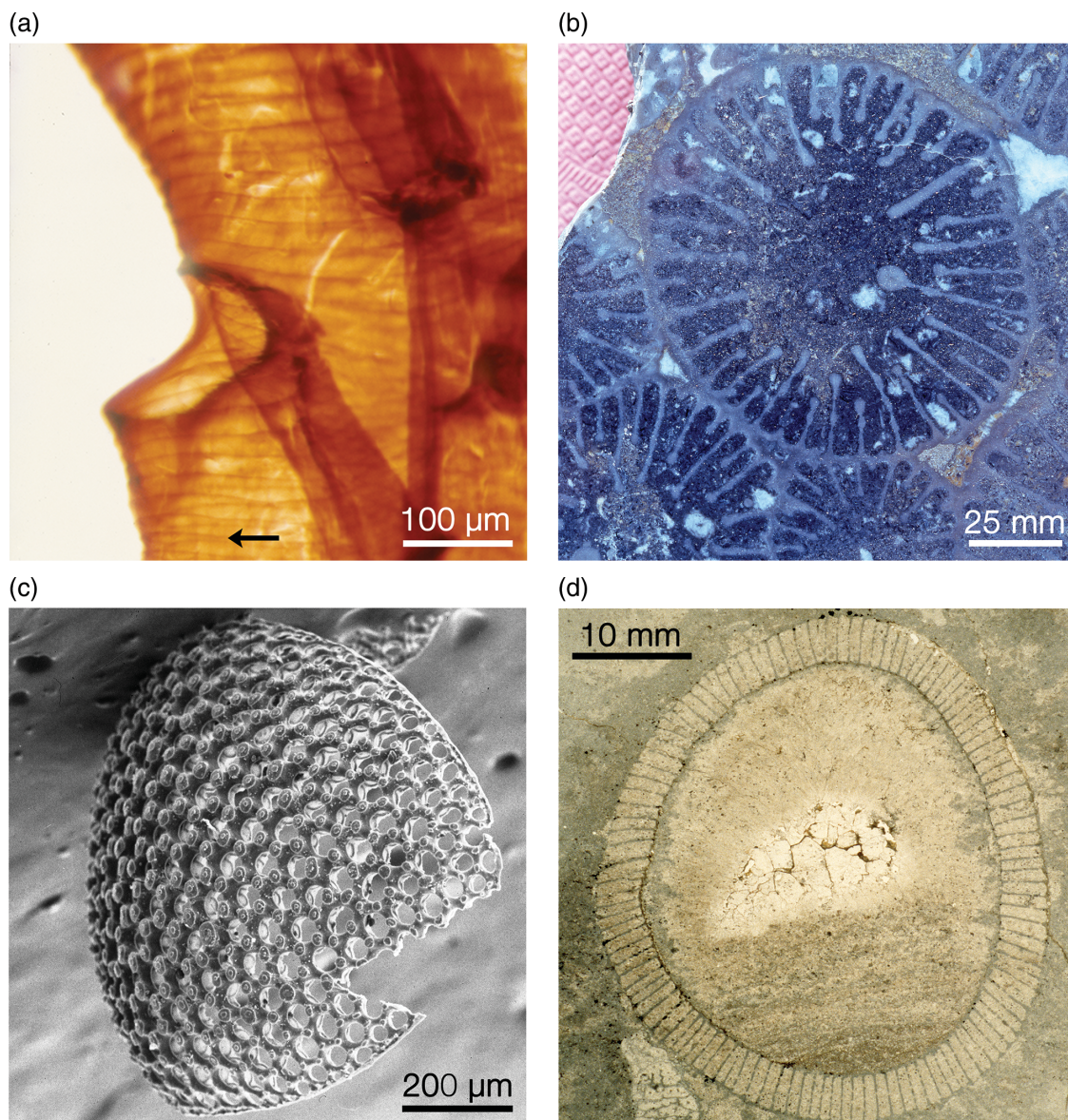


Fig. 11. Previously puzzling Problematica. (a) 3D preservation of Ordovician graptolite *Amplexograptus maxwelli*, Bromide Formation, Oklahoma, showing half-ring construction of periderm (arrow). (b) Coral-like Cretaceous rudist bivalve *Barrettia monilifera*, Florida Formation, Puerto Rico. (c) Phosphatic shoulder pad of Cambrian lobopod *Microdictyon* cf. *robisoni*, Gowers Formation, Queensland. (d) Transverse thin-section of Cambrian regular archaeocyath *Loculicyathus alternus*, Ajax Limestone, South Australia.

photograph of the *Microdictyon* animal from Chenjiang. We both began to laugh; no one could have imagined that *Microdictyon* was the shoulder pads of a lobopodian relative of Conway Morris's *Hallucigenia*. Some answers require new evidence rather than imagination.

Applying these lessons to the Ediacaran fossils may help find their place in the tree of life. Here are other guidelines, largely adapted from Dunn & Liu (2019): (1) Know that all fossils must be connected to some branch of the extant tree of life; they will either be stem or crown members of their respective clades. (2) Work with the best current consensus tree based on phylogenetic information obtained from living organisms. (3) Assume that most early problematical fossils – orphan plesions – will be stem rather than crown members of their respective clades. (4) Avoid terminology that incorporates a preconceived worldview when naming clades. (5) Use data obtained from populations of individuals rather than individual examples whenever possible.

6.c. Phylogenetics

For a phylogenetic framework, I assume that a monophyletic Porifera rather than Ctenophora is the basal branch of the metazoan tree and that xenocoelomorphs are simplified relatives of echinoderms and chordates (Kapli & Telford, 2020). The latter assumption leaves a clean Bilateria of the form (Deuterostomia (Ecdysozoa, Lophotrochozoa)), which is ample for this discussion. I also accept tentatively (Fig. 12) the sibling relationship between Cnidaria and Ctenophora proposed by Zhao *et al.* (2019) based on their careful analysis of putative Cambrian stem members of the Ctenophora; this resurrects a monophyletic Coelenterata for the two phyla, a position adopted by Cavalier-Smith (2017) for entirely different reasons. The evolution of the metazoan stem lineage has been well reviewed by Cavalier-Smith (2017), Brunet & King (2017) and Budd & Jensen (2017); there is nothing to add except to note that Apoikozoa of Budd and Jensen (Choanoflagellata + Metazoa) yields to Choanozoa of Brunet and King.

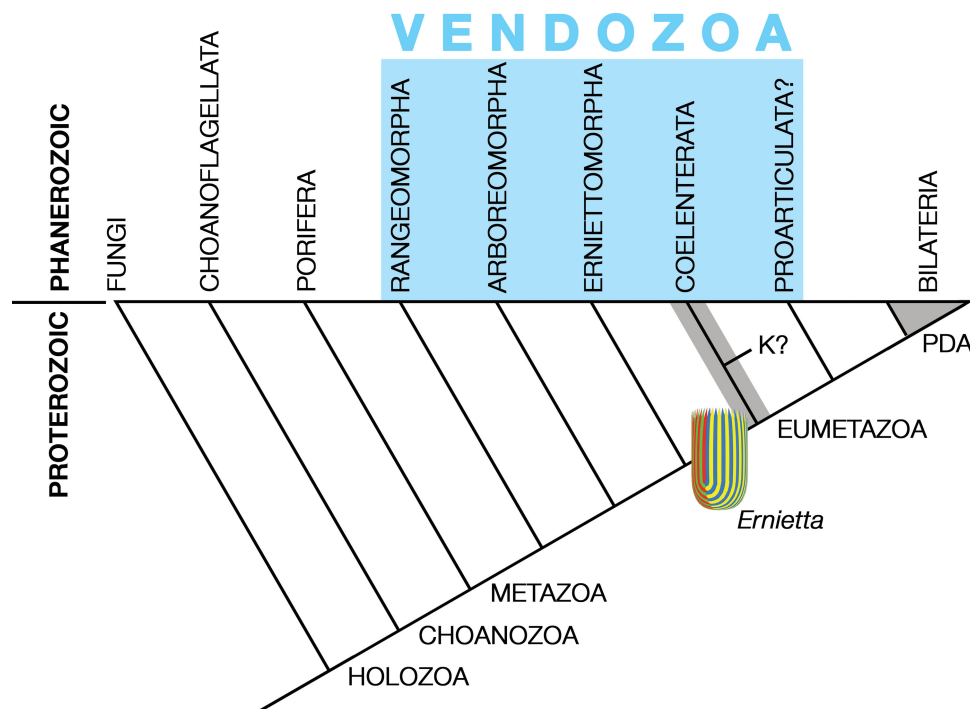


Fig. 12. Best-guess scenario for the relationships of Ediacaran organisms discussed in this review at the time of the Proterozoic–Phanerozoic boundary, when all of the groups shown in blue could have been easily accommodated in Seilacher’s ‘Vendozoa’. Ichthyosporea and Filasterea are omitted but lie between Fungi and Choanoflagellata; for the Metazoa, Porifera is treated as both basal and monophyletic, Placozoa (not shown) probably falls somewhere between sponges and coelenterates and Coelenterata consists of the sister phyla Cnidaria and Ctenophora, which may be either a clade (line) or a grade (shading). *Ernietta* is highlighted because it illustrates the degree of complexity that may have led to the early diverging eumetazoan phyla. The position of the Proarticulata is uncertain as it depends on whether or not its members had an alimentary canal (blind or through gut). If not, they should be lower in the diagram. K? stands for *Kimberella*, which as explained in the text, may have been a kind of foraging coelenterate; PDA is the protostome–deuterostome ancestor.

There is a continuing consensus that rangeomorphs and arboreomorphs are of cnidarian grade (Table 1), being constructed from inner and outer layers of cells with a collagenous structural layer of some sort in between. Cavalier-Smith (2017) suggested that this architecture could be pre-sponge, formed of layers of choanocytes on all unattached surfaces, but Dufour & McIlroy (2017, 2018) thought this unlikely and instead proposed a pre-placozoan alternative with phagocytic cells on surfaces that are not exposed to ocean water. Similar ideas were foreshadowed by Pflug (1972a). Given the architectural complexity of rangeomorphs and arboreomorphs in comparison with sponges, including the Archaeocyatha, a pre-placozoan or pre-cnidarian grade seems more likely. As a starting point, rangeomorphs and arboreomorphs are placed somewhere between sponges and coelenterates on the metazoan tree (Fig. 12). Budd & Jensen (2017) arrived at a similar conclusion but put rangeomorphs beneath the Porifera.

That is the easy part. But is it possible to use any of the other core Ediacarans to show how more complicated animals might have evolved? Glaessner and Wade apparently thought not: ‘The Ediacara fauna in general appears too young to be the repository of links between many phyla. Coelenterates, annelids and arthropods were quite diversified by that time (Glaessner 1971)’ (Wade, 1972a, p. 189). This was prior to the use of molecular clocks to estimate divergence times (e.g. Dohrmann & Wörheide, 2017), but given the fact that stem ecdysozoans must date from at least the time of the first appearance datum (FAD) of *Treptichnus pedum* Seilacher, 1955 (Kesidis *et al.* 2019) and that the terminal Ediacaran worm *Sabellidites cambriensis* Yanishevsky, 1926 may be a crown group annelid (Moczyłowska *et al.* 2014; but see Georgieva *et al.* 2019), the same concern may still apply. On the

other hand, Zhao *et al.* (2019) appear to have demonstrated considerable evolution of body form within the Cambrian in animals of coelenterate grade, so perhaps the game was not over by the later Ediacaran.

Two transformations in animal body plan that may be detectable in Ediacaran biology are the appearances of the cnidarian coelenteron and the bilaterian gut. These are traditionally attributed to larval innovations, as elegantly summarized in verse by Walter Garstang (1966). However, even though Haeckel’s (1874) gastraea theory was derived from a sponge gastrula, the atrium (spongocoel) of sponges is not likely to be homologous with the coelenteron of cnidarians (Nielsen, 2008). Cavalier-Smith (2017) disagreed, arguing that the inside of a simple asconoid sponge is the forerunner of the cnidarian coelenteron. To some extent, this proposal resembles Pflug’s petaloid cavity or ‘centrarium’ in that an enclosed piece of the open environment is co-opted for a body cavity. Cavalier-Smith then took the extraordinary step of transforming the cnidarian coelenteron into the bilaterian coelom by extending the pharynx into a gut that pierced the aboral body wall, creating an anus (Cavalier-Smith, 2017, fig. 3).

There may be another pathway to the cnidarian coelenteron that bypasses sponges completely. Imagine *Ernietta* as a stem cnidarian with the modules filled with mesenchyme, as envisaged by Dufour & McIlroy (2017), and with seams between modules that will eventually become the mesenteries of an anthozoan polyp. The tapered growing ends of the modules may then have acquired nematocysts and became more muscular, allowing the animal to begin to collect higher quality food than previously possible. Furthermore, the bipolar symmetry of *Ernietta* may be superficial, given its close resemblance to *Pteridinium* and to a lesser extent *Phyllozoon* (Figs 3,

6; Gehling & Runnegar, 2021). If so, cnidarians may have inherited ‘bilaterian’ body axes (L–R, A–P, D–V) from erniettomorphs.

Phylogenomic studies support a monophyletic Cnidaria comprising two principal clades, Anthozoa and Medusozoa (Hydrozoa + (Staurozoa, Scyphozoa, Cubozoa)), and characterize the ancestral cnidarian as a solitary, non-symbiotic polyp that propagated by means of a planula larva (Pratlong *et al.* 2017; Kayal *et al.* 2018; Khalturin *et al.* 2019). Although (Khalturin *et al.* 2019) felt that the genetic and morphologic differences between anthozoan and medusozoan body forms were too great to support anything more complicated than a planula as their mutual last common ancestor, the presence of conserved *minicol-lagen* gene clusters, the products of which encode the principal structural protein of nematocytes in all major cnidarian clades, is an indication that the ancestor must have been large enough to need and use nematocysts. This argues for extreme divergence of current polyp architecture rather than a larval level latest common ancestor (LCA).

All anthozoans, including Palaeozoic rugose corals (Fig. 8b), are bilaterally symmetrical (Oliver, 1980). In the model anthozoan, the starlet sea anemone *Nematostella* Stephenson, 1935 (Frank & Bleakney, 1976), the bilateral symmetry is expressed first in the early planula larva by an elongation of the oral opening and then by the disposition of the first eight mesenteries and the formation of the first four tentacles, two on either side of the symmetry plane (He *et al.* 2018). Subsequently, one end of the oral aperture becomes enlarged to form a ciliated groove (siphonoglyph), which serves as a landmark during further development. Thus, *Nematostella* and other anthozoans have a vectorial ‘directive axis’ that lies in the plane of symmetry (Fig. 8b). This axis expresses the products of some *Hox* and other positional genes during development and is therefore equated with the anterior–posterior axis of bilaterians (He *et al.* 2018; Nielsen *et al.* 2018; Technau & Genikhovich, 2018). It follows that the oral–aboral axis of cnidarians is equivalent to the ventral–dorsal axis of bilaterians and perhaps to the lower and upper surfaces of *Trichoplax*, respectively (DuBuc *et al.* 2019). This 3D Cartesian coordinate system predates at least the coelenterates in metazoan evolution and may have been present in classic Ediacarans, including all of the taxa reviewed here. If so, how can this help us understand Ediacaran palaeobiology?

The two principal proposals for the derivation of the bilaterians from coelenterates are Haeckel’s (1874) gastrea hypothesis and von Graff’s paedomorphic planula hypothesis (Hejnl & Martindale, 2009). Each requires larval adaptations that are expressed as new kinds of adults. In Haeckel’s case, the archenteron of the larva, which resulted from gastrulation, becomes the gut of the adult. In protostomes, the oral aperture of the larva becomes the mouth, whereas in deuterostomes it becomes the anus. This problem of initial order was overcome by Sedgwick’s (1884) amphistomy hypothesis, which derived the mouth and anus from opposite ends of an elongate blastopore; loss of one or other larval apertures then accounted for the protostome–deuterostome division (Nielsen, 2008; Hejnl & Martindale, 2009). Nielsen *et al.* (2018) have advanced a strong case for early amphistomy, whereas Hejnl & Martindale (2009) have equally firmly rejected both amphistomic gastrulation and Haeckel’s gastrea. Nevertheless, amphistomic gastrulation helps solve the topological problem of deriving the A–P axis of a bilaterian from the directive axis, rather than the oral–aboral axis, of a coelenterate.

For the Ediacaran White Sea biota, these matters were investigated by Fedonkin (1985a,b) using the principles of

promorphology (animal symmetry) expounded by Beklemishev (1969). However, in contrast to Sedgwick (1884), who suggested that the bilateral symmetry of an annelid is inherited from amphistomic development in the directive plane of an anemone, Fedonkin thought that the Ediacaran ‘medusoids’ were jellyfish of various symmetry classes (infinite, infinite and radial, uncertain, three-fold, four-fold, etc.) that led directly to the more elongated but still somewhat radially arranged Proarticulata (*Dickinsonia et al.*). Thus, the glide symmetry of proarticulates represented an early attempt to transform radial elements into metameres, and the anterior–posterior axis of bilaterians was developed during this process. A similarly vague derivation was proposed by Malakhov (2016, p. 295), who speculated that ‘it was the mobile mode of life [of Ediacaran proarticulates] that determined the development of antero-posterior polarity and bilateral symmetry in the common ancestors of Cnidaria and triploblastic Bilateria.’ This scenario is more clearly described by Arendt *et al.* (2015), who treated the ‘gastric pouches’ of *Dickinsonia* (Dzik, 2003, fig. 8; sediment-filled modules, as discussed in Section 5.c) and the compartments defined by the four pairs of mesenteries of a *Nematostella* ‘edwardsia larva’ (Daly, 2002), as homologous structures. They also suggested that the terminal addition of modules in *Dickinsonia* (Runnegar, 1982; Gold *et al.* 2015; Ivantsov *et al.* 2020) and mesenteries in anthozoans have a common developmental origin. The implication here is that the vagile habits of proarticulates are responsible for the directive axis in cnidarians, which is the opposite of what Sedgwick thought.

On the other hand, it may be that the quasi-bilateral symmetry of rangeomorphs, arboreomorphs, some erniettomorphs, and dickinsoniomorphs and their growth by terminal addition *sensu lato* formed the basis, first for coelenterate and then bilaterian symmetry, following Sedgwick’s mechanism. In this case the hold-fasts of fronds, the proximal ends of erniettomorphs and the ‘head’ regions of dickinsoniomorphs are anatomically ‘anterior’ in the bilaterian sense and their growing tips are ‘posterior’. The coelenteron of cnidarians is derived from the ‘centrarium’ of an *Ernietta*-like animal, as previously explained, and evolutionary amphistomy (Nielsen *et al.* 2018), or perhaps evolutionary deuterostomy (Cavalier-Smith, 2017; Steinmetz *et al.* 2017; Nielsen *et al.* 2018; Steinmetz, 2019), then leads to the Bilateria. It is a wild speculation but one that may help focus thinking on the path ahead. The phylogenetic implications of this suggestion are illustrated in Figure 12. According to this theory, those forms with apparently bipolar symmetry, such as *Fractofusus* and *Ernietta*, are secondarily bipolar, having been able to relax the directive axis developmental constraints for lifestyle reasons. Glide symmetry represents a transitional step between the zig-zag axes of rangeomorphs, arboreomorphs, erniettomorphs and proarticulates and the sagittal plane symmetry of the Bilateria. Proarticulates may or may not have had a bilaterian gut, so their phylogenetic position remains uncertain (Fig. 12). *Kimberella* and other Ediacaran taxa not treated here are wildcards that are not easy to place, but there is little evidence to suggest that they were higher in the metazoan tree than coelenterate grade.

7. Envoi

As Breandán MacGabhann (2014) has aggressively noted, there is no such thing as the Ediacara biota; many other complex organisms were around at the same time. Nevertheless, to co-opt an ancient cliché, ‘we recognize it when we see it’. It is in that spirit that we continue to explore the biology and phylogenetic meaning of these fascinating creatures.

8. Methods

The Koch snowflakes (Fig. 8a) were plotted at <https://online.mathtools.com/generate-koch-snowflake>. Aldus Super 3D 2.5 Macintosh OS 9.2 heritage software originally developed by Silicon Beach Software was used to construct the 3D models of *Pteridinium* and *Ernie* shown in Figures 3, 9, 10 and 12. Illustrated specimens are in the following institutional collections: RAS PIN – Borissiak Palaeontological Institute, Russian Academy of Sciences, Moscow; SAM P – Palaeontology, South Australian Museum, Adelaide; UCLA – Earth, Planetary and Space Sciences, University of California, Los Angeles; or in private hands (Fig. 9a).

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