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Reassessment of the Silurian problematicum *Rutgersella* as another post-Ediacaran vendobiont

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Rutgersella is a problematic fossil from the early Silurian (Llandovery) Shawangunk Formation of New Jersey, at first interpreted as a jellyfish comparable with Ediacaran fossils, such as *Dickinsonia*. Three proposed species of *Rutgersella* from the same locality are here regarded as growth or reproductive variants of a single species, *R. truexi*. Sedimentary structures, associated trace fossils and petrographic examination now show that they were sessile organisms of intertidal mudflats. These fossils have been dismissed as pyrite suns, but thin-sections show that they were weakly pyritized, organic structures, with a quilted hollow internal structure, similar to Seilacher's constructional and taxonomic concept of Vendobionta. As for Cambrian *Swartpuntia*, and Devonian *Protonympha*, *Rutgersella* may be a post-Ediacaran vendobiont. The biological affinities of *Rutgersella* are problematic, but are compared with coenocytic green algae, cellular slime moulds, puffball-like fungal fruiting bodies and foliose lichens.

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DISCOVERY of *Rutgersella* in black shales of New Jersey was initially considered significant, because they were regarded as a Silurian holdover of 'Dipleurozoa' (Johnson & Fox 1968). 'Dipleurozoa' is a now-abandoned taxon of bilaterally symmetrical jellyfish erected by Harrington & Moore (1956) for *Dickinsonia* and similar Ediacaran fossils (Fedonkin 1985). Such Ediacaran fossils are now regarded as Vendobionta (Seilacher 1992), but this paper revisits the Ediacaran holdover conclusion of Johnson & Fox (1968). Plausible post-Ediacaran Vendobionta are rare but well documented: Cambrian *Swartpuntia* (Jensen *et al.* 1998) and *Tirasiana* (Crimes & McIlroy 1999, Hagadorn *et al.* 2000, Yang 2010), Ordovician *Rutgersella* (Retallack 2009) and Devonian *Protonympha* (Conway Morris & Grazhdankin 2005, 2006). More controversial are Cambrian *Ediacaria* (Crimes *et al.* 1995), *Emmonsaspis*, *Thaumaptilon* (Conway Morris 1993) and *Stromatoveris* (Shu *et al.* 2006), which are preserved in a different way than Ediacaran vendobionts (MacGabhann *et al.* 2007, Laflamme *et al.* 2013). *Rutgersella*, however, is preserved both in sandstone, like Ediacaran *Dickinsonia* from South Australia (Retallack 2009) and also, as demonstrated here, in pyritic shales, like Ediacaran *Dickinsonia* from Russia (Dzik & Ivantsov 2002, Dzik 2003) and *Aspidella* from Newfoundland

(Gehling *et al.* 2000). This paper, thus, addresses the following questions concerning the enigma of vendobionts. Can *Rutgersella* be included within the Vendobionta? Do vendobionts form a coherent clade with an Ediacaran to Devonian range? What kinds of organisms were Vendobionta?

Pyritization, as found in *Rutgersella*, is a form of permineralization of histology, which has proven revealing for plant fossils (Matten 1973). This paper thus includes a petrographic study of *Rutgersella*, for comparison with other pyritized problematica (El Albani *et al.* 2010). However, pyritization also led Cloud (1973) to dismiss *Rutgersella* as a pyrite sun, and thus a pseudofossil. Cloud's pseudofossil interpretation also is addressed here by comparative taphonomic and petrographic studies.

Materials and methods

Type material of *Rutgersella* was examined in the old Geological Museum of Rutgers University in New Brunswick, New Jersey. Additional material was collected for thin-sectioning and measurement from the locality in Delaware Water Gap and curated in the Condon Collection of the Museum of Natural and Cultural History of the University of Oregon. New collections also allowed precise location of the fossils within a newly measured geological section. Also prepared were petrographic thin-sections and a polished thick-section

of the fossil and associated sediments. A cross-section of *Rutgersella* was also examined with a Helios scanning electron microscope with EDAX chemical analytical capability in the Center for Advanced Materials Characterization (CAMCOR) at the University of Oregon.

Geological setting

Delaware Water Gap is a village named for the valley where the Delaware River flows through a prominent strike ridge of quartzites of the Shawangunk Formation, along the state border between Pennsylvania and New Jersey (Fig. 1). Grey conglomerates and sandstones of the Shawangunk Formation unconformably overlie dark grey shales of the Martinsburg Formation, and are in turn conformably overlain by red beds of the Bloomsburg Formation. *Rutgersella* fossils were found in the Lizard Creek Member of the Shawangunk Formation (Berg & Dodge 1981) at a locality north of the parking lot at 'Point of the Gap Overlook' wayside kiosk (N40.96812° W75.12255°), 1.6 miles southwest of Delaware Water Gap village (Johnson & Fox 1968). This locality is near the base of a thick clastic wedge, and metamorphosed to

lower greenschist facies (Epstein & Epstein 1972). Alteration of conodonts (CAI 4–4.5) and coalified debris (vitrinite reflectance 3.5%) in Silurian rocks of eastern Pennsylvania are evidence of burial temperatures of 190–300°C and burial depths of 6.7–7.9 km (Epstein *et al.* 1977).

Pyritic black shale with *Rutgersella* is at the top of 6 m of grey siltstone and sandstone exposed in woodland below massive cliff-forming sandstones and conglomerates of the upper Lizard Creek Member, 108–113 m above the base of the Shawangunk Formation (Fig. 2). The Lizard Creek Member with its flaser and linsen bedding (Fig. 3D), claystone breccias (Fig. 3C) and mudcracks (Fig. 2) has been considered an intertidal to lagoonal facies of synorogenic, braided stream conglomerates and sandstones (Clarke & Ruedemann 1912, Willard 1928, Swartz & Swartz 1930, Smith 1970, Smith & Saunders 1970).

An intertidal–estuarine palaeoenvironment for *Rutgersella* is also compatible with evidence from other fossils from the same site (Table 1). The eurypterid fauna of this site includes the same mix of walking and swimming taxa as found at Otisville, New York (Plotnick 1999, Tetlie 2007). These have been considered stratigraphically equivalent (Clarke & Ruedemann 1912), but the Otisville beds are stratigraphically higher and equivalent to fish-bearing siltstones within the lower Bloomsburg Formation nearer Delaware Water Gap village (Beerbower & Hait 1959). Fish fragments from the *Rutgersella* site are similar to freshwater forms (*Vernonaspsis* sp. indet. Smith 1970) better known from the non-marine Bloomsburg Formation (Beerbower & Hait 1959). Hints of marine influence come from inarticulate brachiopods (*Lingula* sp.), indeterminate cephalopod fragments (Albright 1987) and a bivalve: the latter found during this study (Fig. 4H), and identified here as *Modiolopsis subcarinata* Hall (1852).

Trace fossils from this locality are evidence of limited marine influence (Metz 1998), especially the widespread ichnotaxon *Arthropycus alleghaniensis* (Fig. 4I), now regarded as feeding burrows (Seilacher 2007) of a marine isopod (McCoy *et al.* 2012). U-shaped burrows of *Arenicolites* sp. (Metz 1998) are characteristic of marine lugworms (Seilacher 2007). Nevertheless, eight ichnogenera (Table 1) represents low behavioural diversity, comparable with non-marine Cambrian–Ordovician ichnofossil assemblages (Retallack 2009). In contrast, Late Ordovician (Katian) marine ichnofossils from Cincinnati, Ohio, have been assigned to 24 ichnogenera, including a diverse range of trilobite and echinoderm traces (Osgood 1970) not found at Delaware Water Gap. Diversity of up to 21 ichnogenera is found in Silurian marine rocks of Canada (Pickerill *et al.* 1977, 1988, Narbonne 1984).

One of these trace fossils ('*Chondrites* sp. cf. *C. arbuscula*' of Metz 1998) is very abundant in some beds, but is probably not a fossil burrow system, like genuine feeding burrows of *Chondrites* (Seilacher

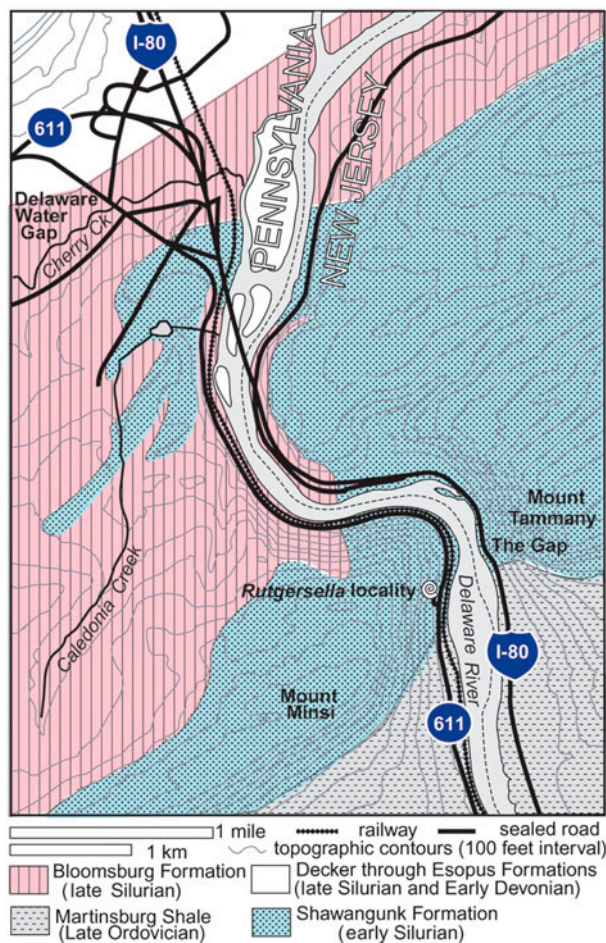


Fig. 1. Locality for *Rutgersella truexi* near Delaware Water Gap, New Jersey. Geological formations are from Berg & Dodge (1981).

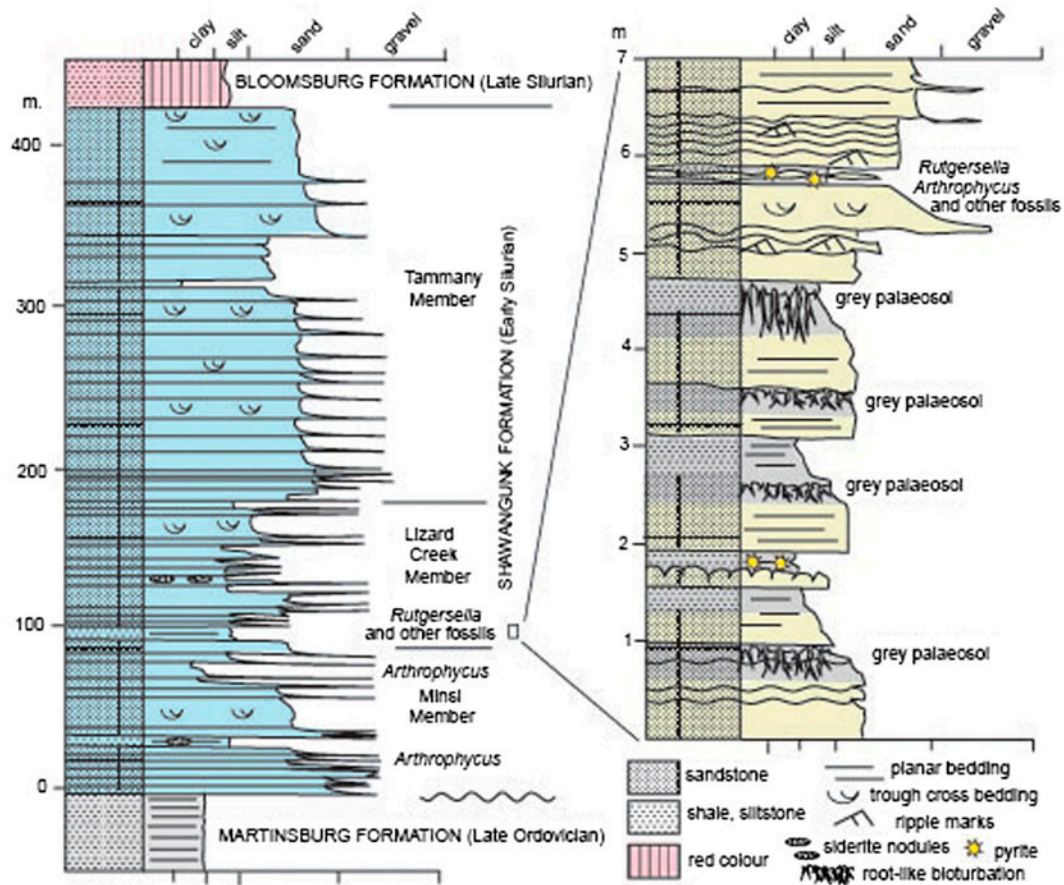


Fig. 2. General stratigraphic section (left) and detailed local section and palaeoenvironmental interpretation of *Rutgersella* horizon (right) in the Lizard Creek Member, Shawangunk Formation, Delaware Water Gap, New Jersey.

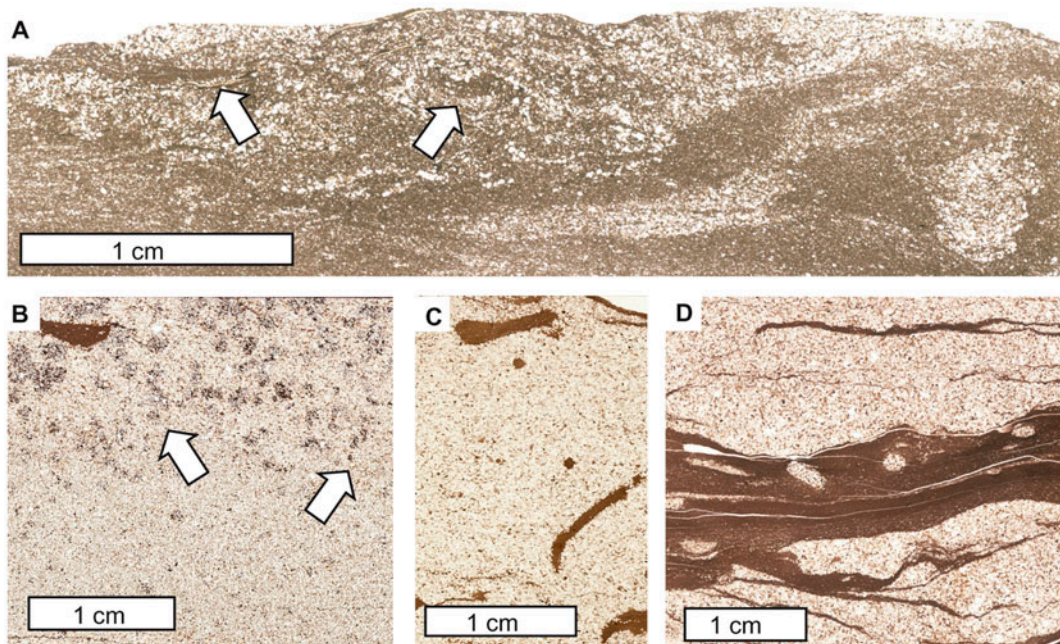


Fig. 3. Petrographic thin-sections of selected rocks from the lower Shawangunk Formation in Delaware Water Gap, New Jersey. **A**, *Rutgersella truexii* (black seams at arrows) in black shale. **B**, Burrow (black shale fill) and indistinct root-like structures in grey palaeosol. **C**, Shale rip-up clasts in sandstone. **D**, Flaser bedding with sand-filled burrows (*Planolites*). All thin-sections were cut vertical to bedding and oriented with upper side uppermost. Specimens in Condon Collection of Museum of Natural and Cultural History, University of Oregon are F116523 (A), F116524A (B), F116524B (C), F116528 (D).

Taxon	Explanation	Source
<i>Rutgersella truexi</i>	Foliose lichen	Johnson & Fox (1968)
<i>Germanophyton psygmyphyloides</i>	Nematophyte corm and squamules	Herein
“ <i>Chondrites</i> . cf. <i>C. arbuscula</i> ”	Nematophyte rhizines	Metz (1998); herein
<i>Palaeophycus tubularis</i>	Horizontal worm burrow	Metz (1998)
<i>Planolites beverleyensis</i>	Horizontal worm burrow	Metz (1998)
<i>Skolithos verticalis</i>	Vertical worm burrow	Metz (1998)
<i>Monocraterion tentaculatum</i>	Vertical worm burrow	Metz (1998)
<i>Rosselia socialis</i>	Vertical worm burrow	Metz (1998)
<i>Arenicolites</i> sp.	U-shaped worm burrow	Metz (1998)
<i>Gordia</i> sp.	Horizontal worm burrow	Herein
<i>Lingula</i> sp.	Inarticulate brachiopod shell	Albright (1987)
<i>Modiolopsis subcarinatus</i>	Bivalve shell	Herein
<i>Protovirgularia</i> sp.	Bivalve trail	Metz (1998)
Cephalopoda	Indeterminate cephalopod	Albright (1987)
<i>Kiaeropterus otisius</i>	Stylonurid (walking) eurypterid	Plotnick (1999), Tetlie (2007)
<i>Hardieopterus myops</i>	Hardieopterid (swimming) eurypterid	Plotnick (1999), Tetlie (2007)
<i>Parahughmilleria maria</i>	Adelophthalmid (swimming) eurypterid	Plotnick (1999), Tetlie (2007)
<i>Hughmilleria shawangunk</i>	Hughmilleriid (swimming) eurypterid	Plotnick (1999), Tetlie (2007)
<i>Erettopterus globiceps</i>	Pterygotid (swimming) eurypterid	Plotnick (1999), Tetlie (2007)
<i>Arthropycus alleghaniensis</i>	Trace of isopod <i>Peralata spinosa</i>	Metz (1998), McCoy <i>et al.</i> (2012)
<i>Vernonaspis</i> sp.	Ostracoderm fish	Smith (1970)
coprolite	Fossil faeces	Albright (1987)

Table 1. Fossils of the Lizard Creek Member, Shawangunk Formation, Delaware Water Gap.

2007). In thin-section, these fossils show no clear wall, inconstant diameter, and appear to be aggregates of filamentous structures (Fig. 3B), like rooting structures of nematophytes (Schaarschmidt 1974, Hillier *et al.* 2008, Retallack & Landing 2014). Corms (Fig. 4J) and radiating phylloids (Fig. 4K–L) referable to *Germanophyton psygmyphyloides* (Krausel & Weyland) Høeg, 1942 were also found during fieldwork for this study at the *Rutgersella* site near Delaware Water Gap. Early Devonian *Germanophyton* is a nematophyte like *Mosellophyton* and *Prototaxites*, as demonstrated by Høeg (1942). Permineralized *Prototaxites* is known from fluvial facies (Boyce *et al.* 2007, Retallack & Landing 2014), but *Mosellophyton* is represented by carbonaceous compressions preserved in place of growth with marine fossils (brachiopods, tentaculites), in low-diversity assemblages comparable with those of modern salt marshes (Schaarschmidt 1974, Schultka & Remy 1990, Wehrmann *et al.* 2010). Although algal affinities have been proposed for nematophytes (Schweitzer 1983, Strother 1988), evidence from charcoaled (Edwards & Axe 2012; Edwards *et al.* 2013) and permineralized specimens (Hueber 2001, Retallack & Landing 2014) and from stable isotopic studies (Boyce *et al.* 2007, Hobbie & Boyce 2010) now indicates that nematophytes were terrestrial lichens (Retallack 1994, Selosse 2002, Edwards *et al.* 2013, Retallack & Landing 2014). Unlike Devonian to modern ascolichens and basidiolichens (Honegger *et al.* 2013a, b), nematophytes may have been a symbiosis of glomeromycotan fungi and green algae (Retallack & Landing 2014).

Shales of the Shawangunk Formation near Delaware Water Gap have been sampled for fossil spores and acritarchs, and found barren, but marine acritarchs were

recovered from the same unit further west in Pennsylvania (Smith & Saunders 1970). Laterally equivalent units in Pennsylvania also include cryptospore tetrads (*Tetrahedraletes medinaensis*) attributed to liverworts, such as sphaerocarpaceans (Gray 1985), as well as trilete spores (*Ambitosporites* sp., *Retusotriletes* sp.) attributed to early vascular land plants, such as rhyniophytes (Johnson 1985, Strother & Beck 1995).

Pseudofossil, ichnofossil or body fossil?

Cloud (1973) dismissed *Rutgersella* as a pseudofossil: specifically as a pyrite sun. Pyrite suns best known to commercial mineral dealers come from Pennsylvanian black shale of southern Illinois, USA (Fig. 5; Bannister 1932, Johnsen 2000, p. 117, Reinertsen *et al.* 1992, Myers & Chenoweth 2010). These are solid pyrite and have a raised central union of straight, strictly radial crystals, in several layers. The ribs of *Rutgersella*, in contrast, curve into an elliptical central region folded into a lower bedding plane. Growth of *Rutgersella* maintains an elliptical shape with a small number of radial segments (Fig. 6), not circular with fine interpolated crystals like pyrite suns. Unlike pyrite suns in southern Illinois (Myers & Chenoweth 2010), *Rutgersella* is not a common fossil at its type locality or elsewhere (Retallack 2009). The five original specimens of Johnson & Fox (1968) were supplemented by collection of six additional measurable specimens (Figs 3A, 4A–F). Three specimens in a single section (Fig. 7) are evidence of a clumped distribution of a generally rare fossil. A thin-section (Fig. 7) and scanning electron microscopy of its billet (Fig. 8) also shows that *Rutgersella* had cavities filled with chalcedony and was

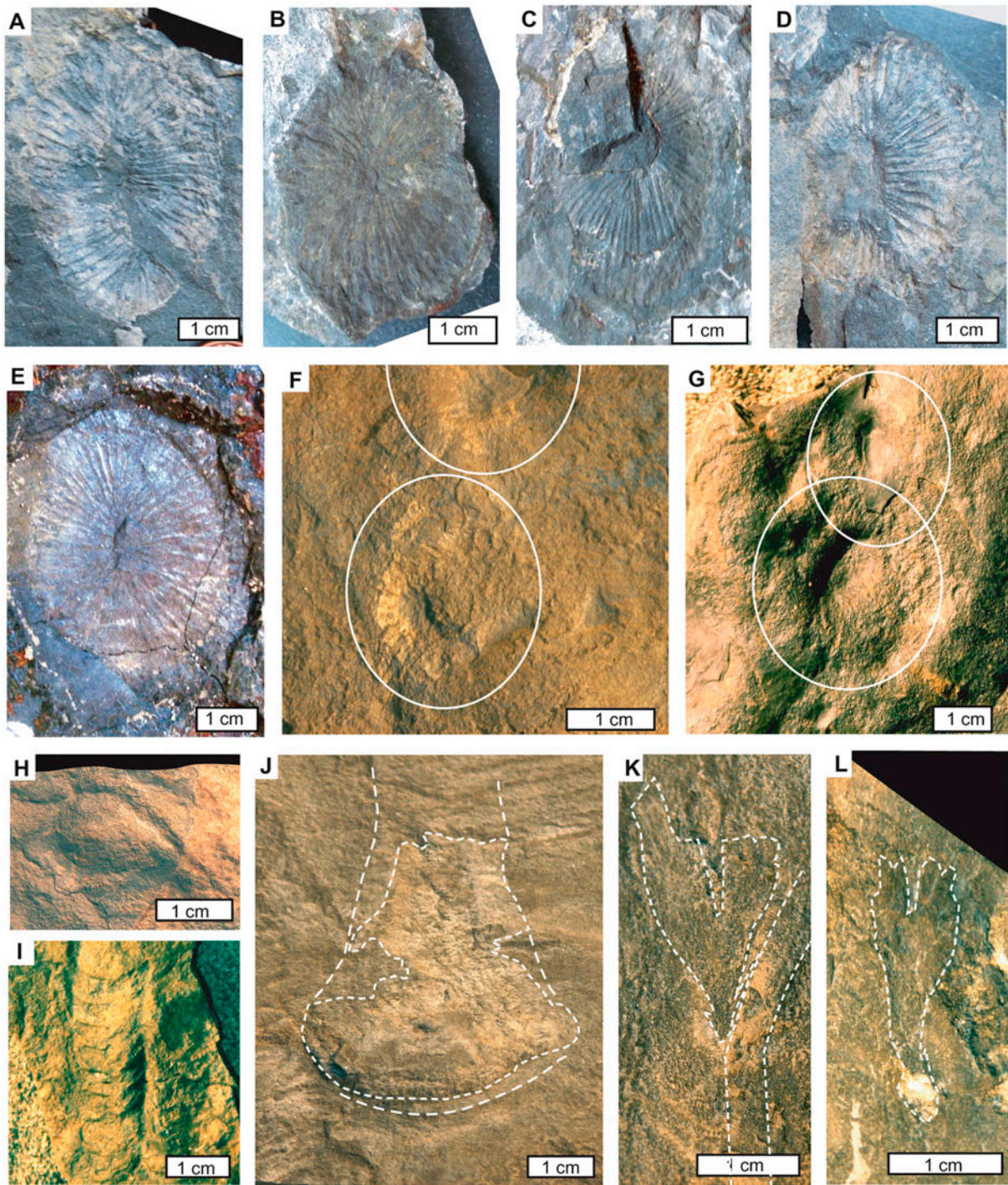


Fig. 4. *Rutgersella* and associated body and trace fossils, all bedding plane views. A–G, *Rutgersella truexi*. A–C, Partly pyritized holotypic black shale specimens of Johnson & Fox (1968). D–E, Additional black shale specimens. F–G, Poorly preserved examples with central poorly preserved pit on dark grey siltstone beds. H, Bivalve *Modiolopsis subcarinatus*. I, Burrow *Arthropycus allegheniensis* from flaser bedded siltstone. J–L, Nematophyte *Germanophyton psymphyloides* corm (J) and phylloids (K–L). Specimen numbers in the Rutgers Geology Museum (A–E) and Condon Collection of Museum of Natural and Cultural History of the University of Oregon (F–L) are 68:5:2 (A), 68:5:3 (B), 68:5:1 (C), 68:5:4 (D), 68:5:5 (E), F116524A (F), F1165224B (G), F116528 (H), F116527 (I), F116318A (J), F116324A (K), F116323A (L).

only lightly pyritized. Semiquantitative analyses of the cavity fill by EDAX on a scanning electron microscope confirmed abundant silicon, with lesser potassium, iron and magnesium of illitized smectite but no calcium or sodium. In addition, fossils of *Rutgersella* have been found in ferruginized sandstone elsewhere with no hint of pyritization (Retallack 2009).

Another similar pseudofossil has been regarded as so life-like that it was given a Latin name, '*Guilielmites*' (Häntzschel 1975). These are radially slickensided nodular or other hard centers created during burial compaction of shales (Byrnes *et al.* 1978). *Guilielmites* has only fine discontinuous radial striae, and lacks the widely spaced grooves of *Rutgersella*. Furthermore,

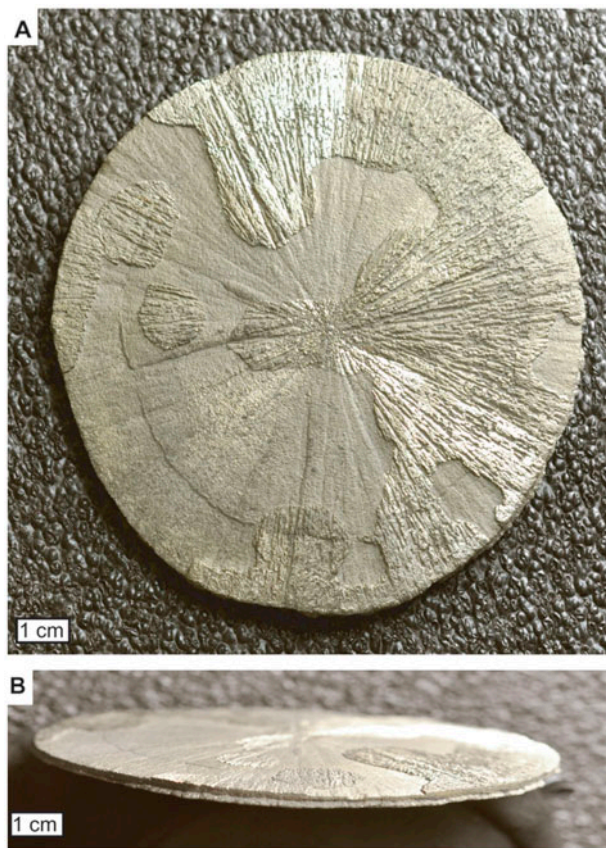


Fig. 5. Pyrite rosette ('pyrite sun') from Pennsylvanian Anna Shale Member, Carbondale Formation, overlying the Herrin (no. 6) coal in Spartan Mine, near Sparta, Randolph County, Illinois: specimen R3924 Museum of Natural and Cultural History, University of Oregon.

Guilielmites is strongly convex with a profile steepening toward the margin, not flat and rumpled like *Rutgersella*. Finally, *Guilielmites* is not a chambered organic structure when viewed in thin-section, but massive and nodular (Byrnes *et al.* 1978).

Rutgersella also has superficial resemblance to radially arranged burrows (Gyrophyllitids of Seilacher 2007) and particularly the ichnogenera *Atollites*, *Brooksella*, *Gyrophyllites*, *Kirklandia* and *Palaeosemaeastoma* (Häntzschel 1975). Like other burrows, their radial segments show little change in diameter, and include meniscate backfills, truncation of bedding and other indications of burrowing. *Rutgersella* shows none of these features in thin-section, and has thick organic walls within sedimentary layering (Fig. 3A, 7A–D). *Rutgersella* was an organic body, which excluded surrounding grains, its cavities filled with chalcedony. Specimens from siltstone beds with algal texture and fossil trails are evidence that it lived at the sediment surface (Fig. 8).

One or three species?

Johnson & Fox (1968) erected three species of *Rutgersella* for their three illustrated specimens

(Fig. 4A–C). Other material shows an array of preservation from three dimensionally pyritized (Fig. 3A) to impressions on beds (Fig. 4F–G). The size and elongation of the central depression, a key feature used to distinguish species by Johnson & Fox (1968), vary, ranging from a small opening in small specimens (Fig. 4B), to moderate in moderate-size specimens (Fig. 4C), elongate in large specimens (Fig. 4A), and both large and elongate in poorly preserved specimens (Fig. 4F–G). The modest increase in size of the central area with overall size (Fig. 6), as well as with deflation and effacement, suggests that the central area grew with some process of maturation. One possibility is that the empty central area was the site of growth of reproductive structures not preserved after propagule dispersal. Another possibility is that the central area was due to necrosis of older parts of a body that enlarged by radial growth. Other *differentiae* between the three species of Johnson & Fox (1968) are the thickness of the organic coating and of folds of the coating that define the radial segments, and degree of crenulation of organic matter. All three of these features decrease with increased size of the central mound, and presumed progression to sexual maturity or central necrosis.

The species concept of Johnson & Fox (1968) was guided by their presumption that *Rutgersella* was a medusa morph of a jellyfish, as was envisaged by Sprigg (1947) for *Dickinsonia*. Such sophisticated animals as jellyfish are distinguished by small differences in gut size (central area) and pellicle thickness and ornamentation (organic coating). Harrington & Moore (1956) recognized that *Dickinsonia* lacked the radial symmetry of jellyfish, and placed them in a distinct class of Cnidarians, the 'Dipleurozoa'. These were not the only differences, so that cnidarian affinities were abandoned as *Dickinsonia* was compared successively with turbellarian (Termier & Termier 1968, Fedonkin 1981), polychaete (Wade 1972) and annelid worms (Conway Morris 1979), xenophyophore foraminifera (Zhuravlev 1993, Seilacher *et al.* 2003), scleractinian corals (Valentine 1992), lichenized or unlichenized fungi (Retallack 1994, 2007) and placozoans (Sperling & Vinther, 2010). *Dickinsonia* has also been referred to problematic extinct taxa of Metazoa (Trilobozoa of Fedonkin 1985) or Protoctista (Vendobionta of Seilacher 1992). Whatever one makes of *Dickinsonia*, and it remains a puzzle (Brasier & Antcliffe 2008), soft-bodied worm and placozoan models are untenable for *Rutgersella*, which has a compaction-resistant, chambered organic pellicle (Fig. 7). Coral interpretations imply a calcareous skeleton (Valentine 1992) and xenophyophore interpretations imply a stercomare (Tendal 1972), and neither were seen in *Rutgersella* (Fig. 7). Protoctistan and fungal models for *Rutgersella* and *Dickinsonia* require chemical and ultrastructural bases for species definition, rather than definitions based on slight differences in external morphology expected of metazoans, especially skeletonized metazoans.

Systematic palaeontology

Kingdom and Phylum INCERTAE SEDIS

Rutgersella Johnson & Fox, 1968

Emended diagnosis. Thick flattened ellipsoidal fossils formed of radiating wedge-shaped elements, laterally coalesced, and meeting along a central trough or basin; segments are numerous, much longer than wide: the upper surface of the radial segments is convex and defined by flanking sulci; outer ends of the radial segments show median sulci and also curve strongly under the body; each radial segment is a hollow organic-walled structure about twice as wide as high, which shares a wall with the neighboring segment; the lower surface is a diffuse zone of carbonaceous filaments reaching down into the substrate.

Comparisons. The diagnosis of *Rutgersella* has been emended from the one given by Johnson & Fox (1968), because their diagnosis did not include information from thin-sections, and inappropriately included comparisons, especially with *Dickinsonia*. Like *Dickinsonia* (Sprigg 1947, Wade 1972, Retallack 2007, Brasier & Antcliffe 2008), *Rutgersella* has both radiating segments and an elongate central zone, which gives the appearance also of bilateral symmetry. Segments of *Rutgersella* are about twice the width at the margin as near the center, whereas segments of *Dickinsonia* flare much less. The segments are offset along a shallow groove in *Dickinsonia* ('glide symmetry' of Fedonkin 1985), but this is not found in *Rutgersella* because the segments are irregularly juxtaposed in a central fold, or are separated by an elliptical depression or central area of sediment. Australian *Dickinsonia* is preserved in ferruginized sandstone, but *Dickinsonia* from the Russian White Sea coast (Fig. 8A) is partly to completely pyritized in grey shale (Dzik & Ivantsov 2002, Dzik 2003), like *Rutgersella*. Unusually elongate and poorly preserved *Dickinsonia*-like fossils from China (Niu 1997) and Devonian *Protonympha* (Conway Morris & Grazhdankin, 2005, 2006) both have a median seam with glide symmetry not seen in *Rutgersella*. An un-named fossil from the Palaeoproterozoic Franceville Formation of Gabon is also similar to *Rutgersella* morphologically in its elongate-radial symmetry, and preservation as pyritic permineralizations in grey lagoonal shales (El Albani *et al.* 2010). *Rutgersella* differs from the Franceville fossils in its more regularly radial symmetry and lack of a curved clavate central structure. Also pyritized in grey shales, although based on specimens oxidized in outcrop, were *Ichnusina* (Debrenne & Naud 1981, Debrenne & Reitner 2001) and *Persimodites* (Hahn & Pflug 1980). *Ichnusina* has more deeply divided outermost rays, and also a suggestion of a

growth zone, unlike *Rutgersella*. These differences are even more striking in the outward dichotomizing segments of *Persimodites*, which is also nearly circular unlike *Rutgersella*.

Rutgersella truxi (Johnson & Fox 1968) emend. (Figs 4A–G, 7A–D)

1968 *Rutgersella truxi* Johnson & Fox 1968, p. 119, fig. 1.

1968 *Rutgersella delawarensis* Johnson & Fox 1968, p. 119, fig. 2.

1968 *Rutgersella kittatinyensis* Johnson & Fox 1968, p. 119, fig. 3.

Holotype. *Rutgersella truxi* specimen 68:5:1, Rutgers Geology Museum, 85 Somerset Street, New Brunswick, New Jersey, USA.

Type locality. Grey shales in steep slope west of 'Point of the Gap Overlook' wayside kiosk (N40.96812° W75.12255°), 1.6 miles southwest of Delaware Water Gap village, Pennsylvania (Johnson & Fox 1968), in the lower Silurian (Llandovery) Shawangunk Formation.

Diagnosis. *Rutgersella* with thick carbonaceous walls, variably decayed within an elliptical central area; 20–70 mm long by 14–46 mm wide, 2–3 mm thick; radial segments number 22–30 near the central area, but the central sulcus becomes sharper toward the edge, where there are 42–60 segments; segments wrinkled radially, and gently undulose concentrically, with sporadic growth interruptions.

Description. *Rutgersella* has the appearance of both radial and bilateral symmetry. Individual segments radiate from a central elliptical area, which is within a lower bedding plane than the upper surface of the fossil. The bilateral symmetry is clearest in deformed specimens (Fig. 4A, D), in which the segments are not continuous across the midline, comparable with 'glide symmetry' of Fedonkin (1985), but perhaps an artefact of crushing.

Rutgersella is a carbonaceous compression, with a thick, wrinkled, organic upper surface in some specimens (Fig. 4A–E) variably deflated in others (Figs 4F–G), and especially clear in thin-section (Fig. 7C–E) and scanning electron micrographs (Fig. 8A, B). Two tiers of hollows divided by a median organic seam lack included sediment, but are variably deformed by crystallization of chalcedony of presumed late diagenetic origin (Fig. 7C–E, 8C). One section (Fig. 7D) reveals pronounced marginal thickening of the central lamina. The chalcedony fibres have inclusions of organic matter and clay, and the hollows in which they crystallized may not have been devoid of

organic matter, now made unrecognizable by acicular crystallization of chalcedony. In all cases, the thickest opaque layer (organic matter and small pyrite framboids) is the upper surface, and the lower surface is less marked, and moulded to the grains of the substrate, with carbonaceous matter projecting downward a short distance between the grains (Figs 7B–E, 8A–F, 9). The uppermost surface thus appears to have been domed, rigid and smooth, the interiors hollow or with less dense tissue, and the lower surface moulded to and attached to the substrate.

Preservation of cellular structure is poor, and consists largely of long tubular cells. The upper surface of the upper wall is finished with dense material, but also has bulging masses some 30 μm across, with porous interiors (Fig. 8B). Some portions of the upper wall (Fig. 8B) and vertical septa (Fig. 8C) show casts of densely entangled tubular cells. In reflected light, the surficial bulging mass has a crude radial structure and the upper wall has palisade-like structure, but the septae, central seam and lower irregular wall have an irregular wispy structure (Fig. 9). This wispy structure is interconnected with septae and central seams, and not an accidental association of independent filamentous microfossils. Within the zone of rhizomorphic disruption below the irregular and thin lower wall (Fig. 9), branching tubular structures of different diameter are encrusted with small clay flakes (Fig. 8D–F).

Measurements. The following measurements have been made on the available seven specimens (mean \pm standard deviation, range): length (39 \pm 21 mm, 17–69 mm), width (29 \pm 13 mm, 14–46 mm), length of central area (10 \pm 4 mm, 7–16 mm), number of segments in central area (25 \pm 3, 22–30), number of segments at margin (48 \pm 5, 42–56).

Reconstruction. My reconstructed palaeoenvironment of *Rutgersella truexi* (Fig. 10) follows previously published reconstructions based on sedimentology (Smith 1970), palaeocurrents (Epstein & Epstein 1972) and palynology (Smith & Saunders 1970, Strother & Beck 1995). Reconstruction of *Germanophyton psygmophylloides* is based on specimens of Krausel & Weyland (1930) and the restoration of Schaarschmidt (1974), which matches observations at Delaware Water Gap more closely than aquatic reconstruction of much larger specimens by Schweitzer (1983). Internal chambering of *Rutgersella* is based on observations made of thin-sections (Fig. 7), thick sections (Fig. 9) and scanning electron microscopy (Fig. 8), which reveal a system of hollow cavities corresponding to radial segments, but transected at various angles and also disrupted by chalcedony growth during burial diagenesis.

Rutgersella is envisaged as a sessile organism of lower tidal flats because of the following observations: 1, thick upper organic walls, but lower wall moulded to

and penetrating the substrate (Figs 7–9); 2, variable inflation and clarity of segmentation attributed to decay in place, more marked in the growth center (Fig. 4A–G); 3, clustered distribution of a relatively rare fossil (Fig. 3A); 4, in some cases, association on the same slabs with a limited array of marine trace and body fossils (Table 1; Fig. 4H–L), but not euryhaline forms, such as articulate brachiopods, trilobites or echinoderms; 5, associated flaser and linsen bedding (Fig. 3D) and mud-chip breccias (Fig. 3C).

Comparison. *Rutgersella* sp. indet. (Fig. 11A; Retallack 2009) consists of ferruginized sandstone impressions from the Early Ordovician (or possibly late Cambrian), fluvial–lacustrine Grindstone Range Sandstone of Wirralpa Station in the eastern Flinders Ranges of South Australia: thus distinct in palaeoenvironment and mode of preservation from the Delaware Water Gap specimens. The South Australian fossils are small (36.7 \pm 2.7 mm long and 24.2 \pm 1.3 mm wide: mean and standard deviation), and lack large central areas and fine divisions of the radial segments, found in New Jersey *Rutgersella* of similar size. These South Australian fossils may prove to be a distinct species, once more informative material is acquired.

A third species of *Rutgersella* may be represented by material figured by Cloud (1973, figs 6–7) from the Cryogenian (*ca* 740 Ma) Sête Lagoas Formation 15 km north-northwest of Sête Lagoas, Minas Gerais, Brazil (Vieira *et al.* 2007). These fossils have unusually wide sulci between radial elements compared with Pennsylvanian and South Australian specimens. They are weakly pyritized in black shale like *Rutgersella* and also, like *Rutgersella*, were regarded by Cloud (1973) as pyrite suns, despite their flexuous segments, deflated centers and elongate form.

Ediacaran holdovers?

Rutgersella is comparable with *Dickinsonia* and a range of other fossils (Fig. 11) that have been assigned to the

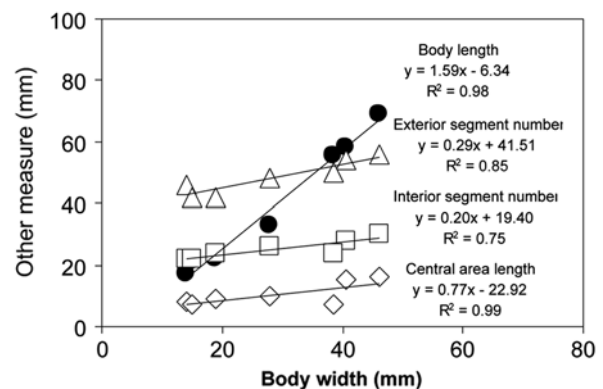


Fig. 6. Measurements of *Rutgersella truexi*, showing orthometric growth.

'Kingdom' Vendobionta by Seilacher (1992, p. 607), with the following definition:

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

Differences in preservation no longer separate Precambrian and Phanerozoic fossils comparable with Vendobionta. Precambrian pyritic-organic preservation of *Dickinsonia* (Dzik & Ivantsov 2002, Dzik 2003) and *Fractifusus* (Gehling & Narbonne 2007) can be matched with pyritic-organic preservation of Phanerozoic *Thaumaptilon* (Conway Morris 1993) and *Rutgersella* (herein). External moulds of Ediacaran *Dickinsonia* in red sandstone (Retallack 2007) are comparable with Cambrian *Swartpuntia* (Fig. 11C; Jensen *et al.* 1998) and Ordovician *Rutgersella* (Fig. 11E; Retallack 2009).

There are also no clear differences between palaeoenvironments of Precambrian and Phanerozoic fossils comparable with Vendobionta. Shallow marine to lagoonal habitats envisaged for some *Dickinsonia* (Dzik & Ivantsov 2002) and *Fractifusus* (Retallack 2014) are matched by habitats envisaged for *Rutgersella* (Fig. 10), although *Dickinsonia* and *Fractifusus* have also been regarded as deep marine (Gehling & Narbonne 2007, Gehling & Droser 2013). My own examination of the sedimentological context and additional collections of Devonian *Protonympha* (Fig. 11G) from Summit and Naples in upper New York state (Conway Morris & Grazhdankin 2005, 2006) confirms intertidal to lagoonal habitats. *Protonympha* is found with only a few inarticulate brachiopods (*Orbiculoidea*) and common fossil plants, including the well-known lycopsid 'Naples tree' (White 1907, Grierson & Banks 1963, 1983, Bonamo *et al.* 1988). Red bed gypsic and calcic palaeosols for other specimens of Precambrian *Dickinsonia* (Retallack 2013) can be matched by similar palaeosols for Cambrian *Swartpuntia* (unpublished observations of localities of Jensen *et al.* 1998) and Ordovician *Rutgersella* (Retallack 2009). Other Cambrian fossils are not universally accepted as vendobionts (Laflamme *et al.* 2013) and are associated with trilobite body and trace fossils, so are more likely marine: *Tirasiana* (Crimes & McIlroy 1999, Hagadorn *et al.* 2000, Yang 2010), *Ediacaria* (Crimes *et al.* 1995), *Emmonsaspis*, *Thaumaptilon* (Conway Morris 1993) and *Stromatoveris* (Shu *et al.* 2006).

Quilted organization is a unifying character of Vendobionta, and pyrite-permineralized fossils, such as *Rutgersella*, now add structural details. There are two layers of chambers with septa alternating around a central seam, so that the impression of segments alternating

at the midrib on the upper surface ('glide symmetry' of Fedonkin 1985) would not be true of the lower surface where segments would continue across the midline. A similar arrangement in Ediacaran *Dickinsonia* may explain the usual appearance of asymmetric alternation at the midrib in impressions of the top (Retallack 2007), but rare degraded or flipped specimens with symmetrical segmentation across the midrib (Gehling & Droser 2013).

The fractal and quilted patterns analyzed by Seilacher (1992) can now be seen to be internal moulds of organic walls, which were unusually resistant to compaction (Retallack 2007). Furthermore, pyritized organic fossils are thin, with a thick, finished upper surface, and thinner, irregular lower surface. More importantly, these pyritized fossils do not support the idea that *Rutgersella* had such sophisticated anatomical features as a gut, mouth, anus or gonads implied by cnidarian or other metazoan affinities (Johnson & Fox 1968). The fractal to quilted organization emphasized by Seilacher (1992) was created by organic walls of organized biological structure, not a stercomare or mineral skeleton (Figs 3A, 7–9). Finally, the histology of *Rutgersella* is imperfectly preserved (Figs 8, 9), but appears most similar to the entangled tubular cells of extinct glomeromycotan lichens, such as *Nematothallus* (Edwards *et al.* 2013) and *Prototaxites* (Retallack & Landing 2014).

Plausible post-Ediacaran vendobionts are all controversial and problematic fossils of uncertain biostratigraphic significance. For example, *Swartpuntia* from the Uratanna Formation of South Australia (Fig. 11C) is above the first appearance of *Manykodes pedum* (Dzik 2005), so is probably of earliest Cambrian age (Jensen *et al.* 1998). However, *M. pedum* is known below the golden spike in Newfoundland (Gehling *et al.* 2001), and a latest Ediacaran age of Uratanna cf. *Swartpuntia* is possible. The 'glide symmetry', or not quite bilateral segmentation of Vendobionta (Fedonkin 1985), such as *Dickinsonia*, is unclear in Palaeozoic *Rutgersella* (Fig. 4A–E), *Thaumaptilon* (Conway Morris 1993) and *Stromatoveris* (Shu *et al.* 2006), and in Ediacaran *Charnia*, *Avalofractus* and *Trepassia*, which have central stalks (Narbonne *et al.* 2009). Seilacher's (1992) constructional model for Vendobionta was chambered, but some were formed from fractal tubular elements (Narbonne 2004), and it is not certain whether this model applies to post-Ediacaran vendobiont-like fossils either. The Vendobionta were originally defined as sessile animals, but supposed 'trackways' (really multiple impressions) of *Dickinsonia*, *Yorgia* and *Epibaion* have been urged as evidence of a motile organism (Ivantsov & Malakhovskaya 2002). Alternatively, these may have been chains of fossils, comparable with fungal fairy rings (Retallack 2007). The various post-Ediacaran fossil genera plausibly assigned to Vendobionta remain as problematic as the Ediacaran fossils.

Perhaps a better way of framing the question is whether Vendobionta was a clade of organisms

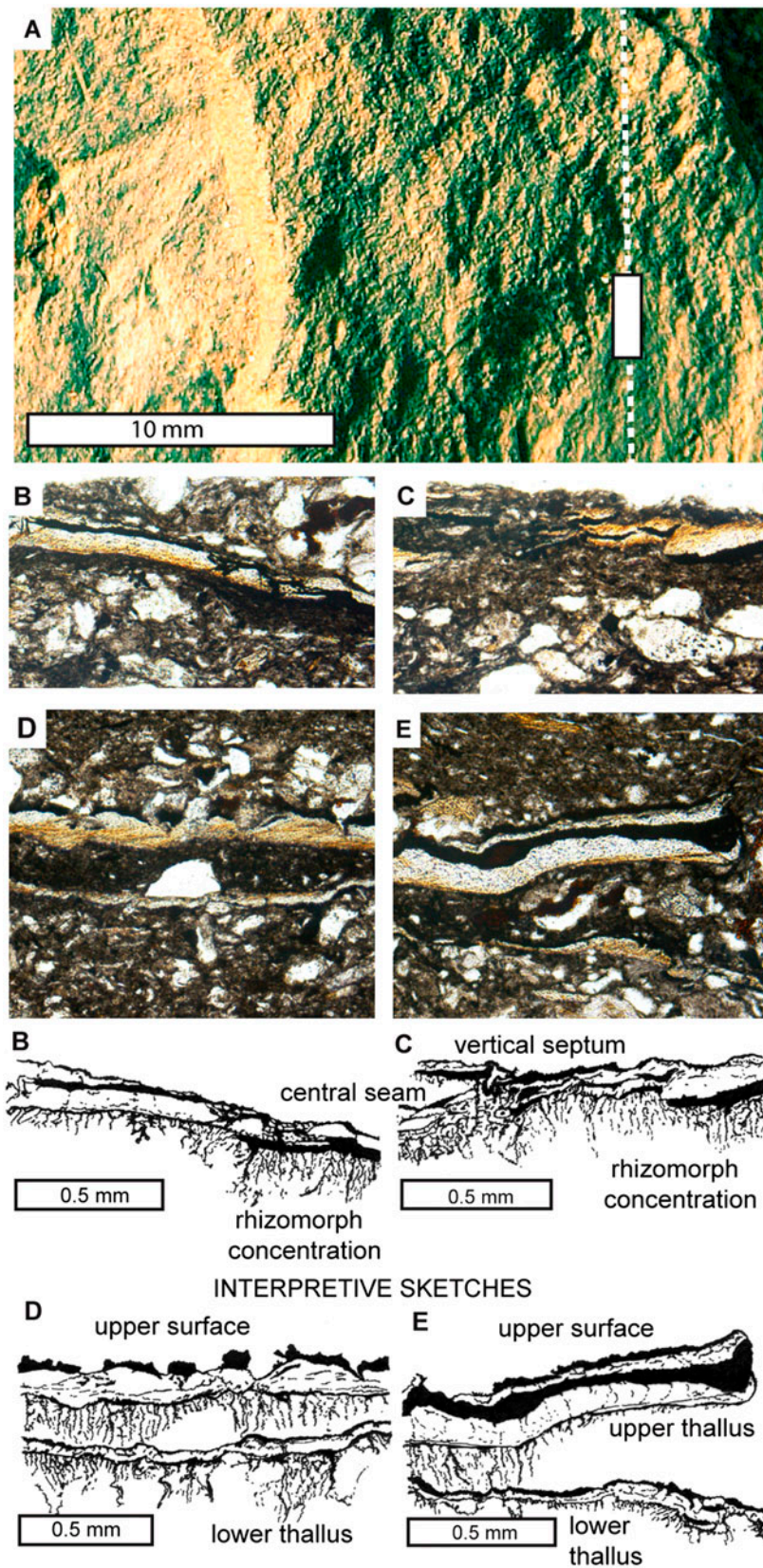


Fig. 7. Petrographic thin-sections of *Rutgersella truexi* (A) cut along the dotted line and mainly within the vertical box: all sections oriented vertical to bedding and with upper surface uppermost, and are cut vertical to the partly covered specimen and perpendicular to its long axis; B–C are exposed and partly covered portions of the exposed specimen; D–E are an additional buried specimen of unknown orientation, but including a lateral margin (E). Photomicrographs are all under plane polarized light. Thin-section in Condon Collection of Museum of Natural and Cultural History at the University of Oregon, F116523.

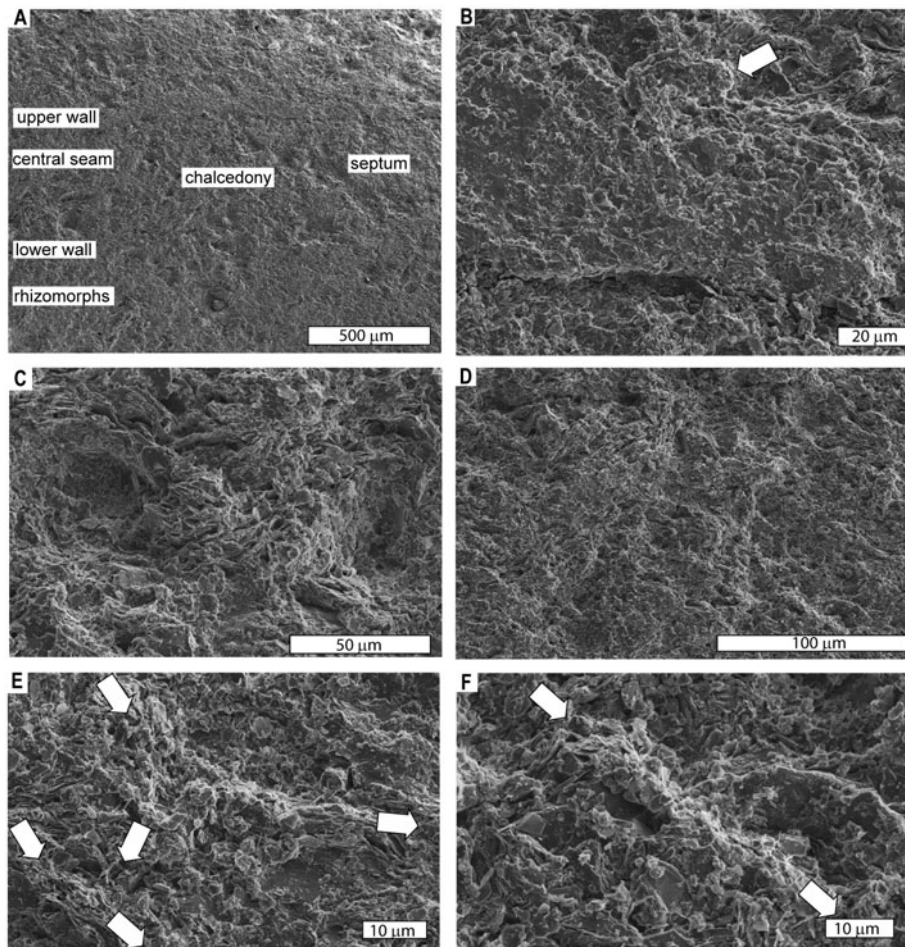


Fig. 8. Scanning electron micrographs of a vertical cross-section of *Rutgersella truexi* all oriented with upper surface to top. **A**, Overview of wall layers seen in Fig. 7C. **B**, Detail of thick upper wall showing surficial hemispherical structure (at arrow) comparable with a cephalodium. **C**, Tubular histology within vertical septum flanked by chalcidony crystals of internal chambers. **D**, Thin lower wall (near top of image) and irregular downward-branching rhizomorphic structures (arrows). **E–F**, Detail of rhizomorphic structure (arrows). Billet in Condon Collection of Museum of Natural and Cultural History at the University of Oregon, F116523.

comparable with a Linnaean Order or Family, or a grade of biological organization like a palaeobotanical form taxon for fossil wood, such as Calamopityales? Like calamopityalean gymnospermous woods (Taylor *et al.* 2009), vendobionts are united by structural similarities, but their reproductive structures, which would be more revealing of relationships, remain unknown. Vendobionta have a distinctive quilting pattern, unlike associated medusiform fossils, which could be microbial colonies of a range of taxa (Bengtson *et al.* 2007, Grazhdankin & Gerdes 2007). Vendobionta may be a grade of extinct organismal organization ranging in age from Ediacaran (Retallack 2013) to Devonian (Conway Morris & Grazhdankin 2005, 2006). Establishing whether this grade of thallus organization is also a clade will require reproductive structures, biochemical or other evidence of biological affinity.

Comparable living organisms

General observations already discussed leave only the following living organisms worth further consideration

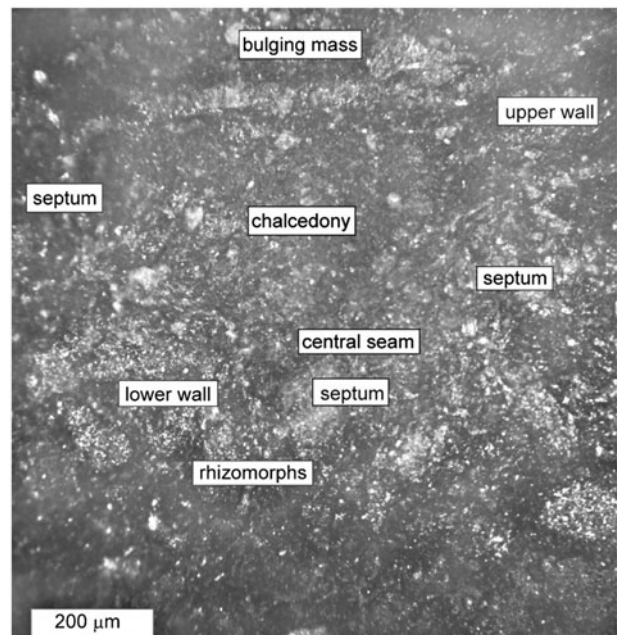


Fig. 9. Polished thick-section of *Rutgersella truexi*, oriented with upper surface to top (same view as Figs 7C and 8A). White grains are pyrite, grey materials are silicates and clay, and black seams are organic matter.

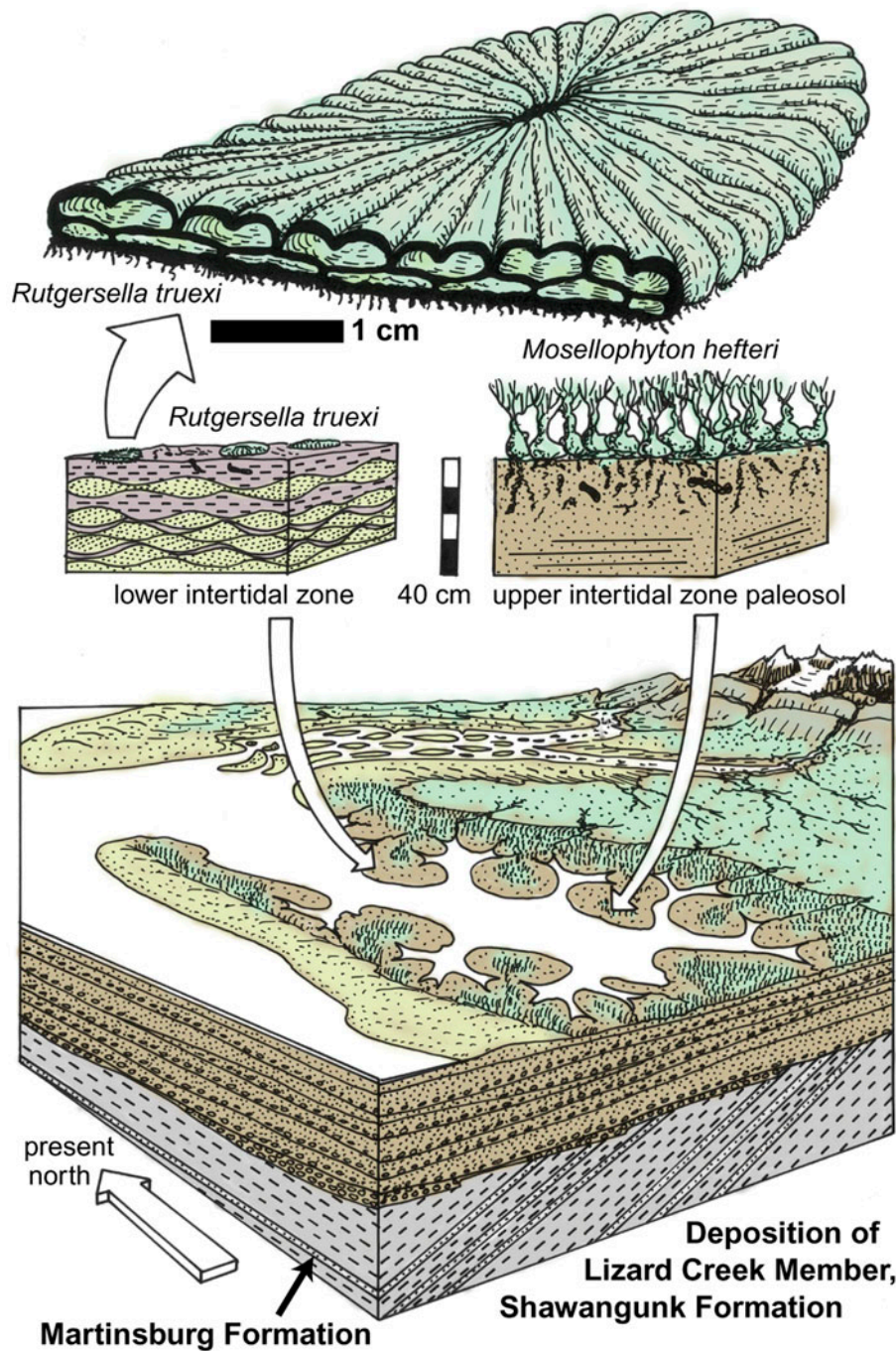


Fig. 10. Reconstructed histology and palaeoenvironment of *Rutgersella truexi*.

as possible modern analogues for *Rutgersella*: algae, slime moulds, unlichenized fungi and lichens.

The radial organization of *Rutgersella* recalls that of siphonous green algae (*Acetabularia*, Dasycladaceae, Chlorophyta) in which coenocytic filaments radiate outwards from a central thread (Graham & Wilcox 2000). Such a thread is not clearly preserved in *Rutgersella*. The thalloid structure of *Rutgersella*, thick on top but irregular and thin below, is unlike dasyclad thalli, which are thick on both sides.

The radial structure of *Rutgersella* is reminiscent of slime moulds, organisms traditionally regarded as fungi

(‘myxomycetes’), but lacking a key synapomorphy of fungi: chitinous cell walls (Brown *et al.* 2009). ‘Slime moulds’ are now regarded as seven distinct clades of eukaryotes (Adl *et al.* 2005). Only the Eumycetozoa (within supergroup Amoebozoa) have megascopic forms and include two kinds of cellular slime moulds (Dictyostelia and Protostelia) and one of plasmodial slime moulds (Myxogastria). Eumycetozoa can be dispersed in the soil as flagellated or amoeboid cells, or as an irregularly shaped multi-nucleate plasmodium or plasmodiocarp (Stephenson & Stempen 1994). Eumycetozoa also produce sporangia, but their central columella gives off a

network of lateral filaments (capillitium) defining crude chambers within an outer thick wall (peridium), unlike the central boss of *Rutgersella*. The aethalium of slime moulds is a sessile cushion-shaped reproductive structure most like the central boss of *Rutgersella*. Although the aggregating phase of cellular slime moulds and the resulting motile slug of cellular slime moulds can appear similar to *Rutgersella*, these were an ephemeral phase in the life cycle. *Rutgersella* in contrast shows different stages of decay (Fig. 4A–G), as if they were persistent sessile organisms.

Unlichenized fungi comparable with *Rutgersella* include puffballs or bird nest fungus (Arora 1986). Could the central area be fruiting bodies such as peridioles or an anchoring stalk? This seems unlikely because these ephemeral fruiting structures decay completely after dispersing spores, whereas old examples of *Rutgersella* persisted after burial by sedimentary laminae, which supported later ones in overlying layers (Figs 3A, 7).

Lichens have various structural similarities with *Rutgersella*. Lichens have cortical-medullary tissue organization of filamentous hyphae, with a thick upper side and thin irregular lower side in crustose lichens and two thick sides in foliose lichens (Brodo *et al.* 2001), the latter most compatible with observations in thin-section (Fig. 7A–D). Radial segments in lichens represent growth axes of thallus expansion, and also are apparent in *Rutgersella*. Lichen thalli also may show concentric constrictions of growth increments, also seen in some *Rutgersella* (Fig. 4C). Some lichens, such as *Lobaria pulmonaria*, have areolate pseudosegmentation (Brodo *et al.* 2001), like the internal partitions of *Rutgersella*. Hyphal histology of lichens, especially extinct Siluro-Devonian lichens (Edwards *et al.* 2013, Retallack & Landing 2014), is also compatible with

observations of clay-encrusted elongate features within the walls and rhizomorphic structures below (Figs 8, 9). A bulging structure seen on the upper wall of *Rutgersella* (Figs 8B, 9) is comparable with a cephalodium of lichens (Brodo *et al.* 2001). The featureless central area, which increases in size with overall size of *Rutgersella* (Figs 4F, G, 6), may represent central necrosis or development of central reproductive structures, which are both common in lichens (Brodo *et al.* 2001).

Lichen is not a taxonomically informative term, because it includes lichenized Basidiomycota, Ascomycota and Actinobacteria (Hawksworth 1988) and in the fossil record perhaps also Glomeromycota (Retallack *et al.* 2013a, b) and Mucoromycotina (Taylor *et al.* 1997, Yuan *et al.* 2005). Although lichens are widely considered limited to rock and bark, numerous lichens colonize soils, especially desert soils, where competition from vascular land plants is limited by shortage of water (McCune & Rosentreter 2007, Retallack 2009). *Rutgersella* would not be the oldest known lichen: it was preceded by an un-named Ediacaran phosphatic fossil from Weng'an China (Yuan *et al.* 2005). Early Silurian palynofloras of Pennsylvania include large leiospheres of plausible mucoromycotinan or glomeromycotan affinities, like Glomalean vesicles from Ordovician rocks of Wisconsin (Redecker *et al.* 2000). Ascomycotan and basidiomycotan spores are absent from Silurian rocks of Pennsylvania (Smith & Saunders 1970, Johnson 1985, Strother & Beck 1995). Current phylogenetic analyses of fungi postulate a Precambrian fossil record for Mucoromycotina–Glomeromycota, but Early Devonian advent of Ascomycota–Basidiomycota (Berbee & Taylor 2010). These molecular biological predictions are confirmed by Early Devonian fossils of both ascolichens and basidiolichens (Honegger *et al.* 2013a, b).

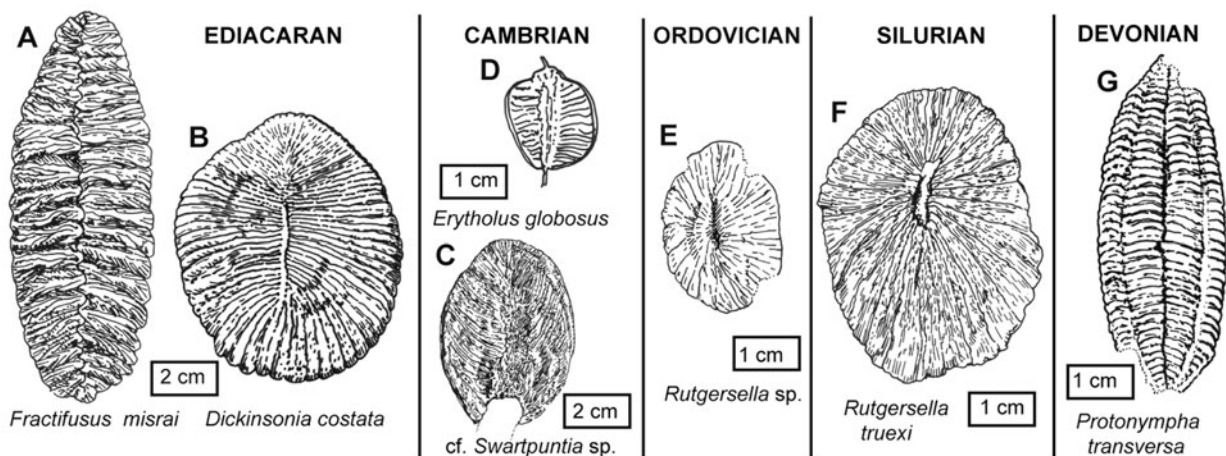


Fig. 11. Ediacaran vendobionts (A–B) compared with possible Phanerozoic holdovers (C–G): A, Middle Ediacaran (565 Ma), Mistaken Point Formation, Mistaken Point, Newfoundland (Gehling & Narbonne 2007); B, Late Ediacaran (555 Ma), Zimny Gory Formation, Zimny Gory, Russia (Fedonkin 1985); C, Early Cambrian (540 Ma), Uratanna Formation, Mudlapena Gap, South Australia (Jensen *et al.* 1998); D, Middle Cambrian (509 Ma), Moodlatana Formation, Wirrealpa, South Australia (Retallack 2011); E, Early Ordovician (483 Ma), Grindstone Range Sandstone, Wirrealpa, South Australia (Retallack 2009); F, Early Silurian (440 Ma), Shawangunk Formation, Delaware Water Gap, Pennsylvania (Johnson & Fox 1968); G, Middle Devonian (387 Ma), Moscow Formation, Summit, New York (Conway Morris & Grazhdankin 2006).

Conclusions

This comparison of *Rutgersella* with other megafossils and with living organisms remains uncertain of biological affinities, but does suggest testable hypotheses. These fossils fall within the extinct group Vendobionta (Seilacher 1992), here regarded as a grade of thallus organization extending from the Ediacaran (Retallack 2007) to the Devonian (Conway Morris & Grazhdankin, 2006). Vendobionta have been compared with metazoans, such as jellyfish (Fedonkin *et al.* 2008), but an organism does not have to be as sophisticated as a metazoan to be megascopic, as can be seen from examples discussed of large coenocytic algae, the episodic multicellular aggregates of slime moulds and the microbial consortia loosely known as lichens. Affinities of *Rutgersella* are constrained by the following evidence. It was a sessile organism of tidal flats. Its upper organic walls are thick and domed, but lower wall had extensions penetrating the substrate. Its histology consisted of tubular cells similar to hyphae, entwined within walls and septa, and bundled into branching lower rhizomorphs. They appear to have decayed in place with a necrotic center, as indicated by variable inflation and clarity of segmentation. They were rare fossils with a highly clumped distribution. They are found with a limited array of marine trace and body fossils, but not fully marine forms. These varied constraints and the structure of *Rutgersella truexi* are compatible with interpretation as a foliose lichen, similar to modern lichens, such as *Xanthoparmelia plittsi*. Its intertidal habitat was similar to other living intertidal lichens, such as *Verrucaria arctica* (Brodo *et al.* 2001). Because a broadly similar body form is found in a variety of lineages of lichenized fungi (Brodo *et al.* 2001), the Vendobionta is regarded as a grade of organisms rather than a clade, pending evidence to the contrary from biochemistry and reproductive structures. Inclusion of Vendobionta within Ascomycota or Basidiomycota seems doubtful considering their later appearance in the fossil record (Berbee & Taylor 2010, Honegger *et al.* 2013a, b). Glomeromycota and Murcoromycotina are known from rocks of similar age (Redecker *et al.* 2000, Yuan *et al.* 2005, Retallack *et al.* 2013a, b), but are not yet demonstrated for Vendobionta or *Rutgersella*, which remain biologically enigmatic.

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