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REVIEW PAPER

Acritarch Evidence for an Ediacaran Adaptive Radiation of Fungi

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ABSTRACT

Acritarchs are problematic organic-walled microfossils, traditionally regarded as phytoplankton, but also as cysts of metazoans or mesomycetozoans, and fungi. This review develops criteria for distinguishing these alternatives, and documents fungal features in several Precambrian acritarchs: (1) irregular shape, (2) hyphal attachment, (3) spherical wall protrusions, (4) septate and fused hyphae, (5) multilayered brittle walls that split and detach, (6) large size (>100 μm), and (7) chitin and chitosan composition revealed by FTIR. Large acritarchs with fungal features are common and diverse during the Ediacaran, at the same time as extinct lichenlike Vendobionta. A different assemblage of small acritarchs diversified with the Cambrian evolutionary explosion of algae and metazoans. A fossil record of glomeromycotan fungi back to the Paleoproterozoic (2200 Ma) supports the idea of fungal life on land long before land plants, and an amended version of Pirozynski and Malloch's mycotrophic origin of early land plants.

Keywords: acritarch, Ediacaran, Glomeromycota, FTIR, wall ultrastructure

РЕЗЮМЕ

Реталлак Г.Дж. Акритархи подтверждают адаптивную радиацию грибов. Акритархи – проблемные микрофоссилии с органическими клеточными стенками, традиционно рассматриваются как фитопланктон, а также как цисты многоклеточных организмов, мезомицетов и грибов. Данный обзор предлагает критерии для различения этих групп организмов и анализ признаков нескольких групп докембрийских акритарх: (1) неправильная форма, (2) крепление гиф (3) сферические выступы клеточных стенок, (4) цельные гифы и гифы с перегородками (5) многослойные хрупкие и расслаивающиеся покровы (6) большой размер (> 100 мкм) и (7) содержание хитина и хитозана, выявляемое инфракрасной спектроскопией. Большие акритархи с признаками грибов обычны и разнообразны в эдиакарской биоте, в то время как лихеноподобные организмы малочисленны. Сообщества небольших акритарх достигли наибольшего разнообразия во время кембрийского эволюционного взрыва водорослей и многоклеточных. Находки окаменелостей гломеромицетов вплоть до палеопротерозоя (2200 млн лет) поддерживают идею распространения жизни на суше в виде грибов задолго до наземных растений и говорят в пользу версии происхождения ранних наземных растений от микотрофных организмов, согласно Пирозинскому и Маллоку.

Ключевые слова: акритархи, эдиакарский период, гломеромицеты, инфракрасная спектроскопия, ультраструктура клеточных стенок

Переведено редколлегией

INTRODUCTION

Molecular clocks now place the antiquity of fungi at about 2500–1000 Ma (Taylor & Berbee 2006, Blair 2009, Berbee & Taylor 2010). Other evidence for Proterozoic fungi have come from fossil compressions such as 2200 Ma *Diskagma* (Retallack et al. 2013a), and 1480 Ma *Horodyskia* (Retallack et al. 2013b), permineralizations such as 2600–575 Ma *Eomycetopsis* (Mendelson & Schopf 1991, Altermann & Schopf 1995), and Vendobionta such as 565 Ma *Fractifusus* (Peterson et al. 2003, Gehling & Narbonne 2007) and 550 Ma *Dickinsonia* (Retallack 2007, 2013a). All these records are taxonomically unsatisfactory because they do not preserve microscopic reproductive structures of fungi, so a more promising source of biological information is the suggestion of Pirozynski (1976), Hermann (1979), Locquin (1983), Burzin (1993) and Butterfield (2005) that there is a Precambrian record of fungi among the enigmatic microfossil palynomorphs known as acritarchs (Grey 2005, Moczydłowska et al. 2011). This study follows the approach of Butterfield (2005) in reviewing benchmarks in the fossil record for particular fungal and animal-fungal characters, including hyphal attachment and fusion, bulbous wall protrusions, and brittle fracture. Also included is discovery of multilayered wall ultrastructure viewed by TEM and chitin composition revealed by FTIR (Table 1). This study also

Table 1. Sources of FTIR spectra

Species	Higher taxon	Age	Reference
Multifronsphaeridium pelorum	"acritarch"	Ediacaran	Arouri et al. 1999
Leiosphaeridium jacutica	"acritarch"	Ediacaran	Marshall et al. 2005
Satka squamulifera	"acritarch"	Ediacaran	Marshall et al. 2005
Shuiyousphaeridium macroreticulatum	"acritarch"	Ediacaran	Marshall et al. 2005
Botryococcus braunii	"acritarch"	Permian	Lin & Ritz 1993
Tasmanites punctatus	"acritarch"	Permian	Lin & Ritz 1993
Mucor rouxii	Mucorales, Zygomycota	modern	Wu et al. 2005
Rhizopus stolonifer	Mucorales, Zygomycota	modern	Kaminskyj et al. 2008
Fusarium avenaceum	Hypocreales, Ascomycota	modern	Calderón et al. 2009
Metapenaeopsis dobsoni	Decapoda, Arthropoda	modern	Sini et al. 2007
Bombus terrestris	Hymenoptera, Arthropoda	modern	Matján et al. 2007
Protoceratium reticulatum	Gonyaulacales, Dinoflagellata	modern	Domenighini & Giordano 2009
Symbiodinium microadriaticum	Suessiales, Dinoflagellata	modern	Domenighini & Giordano 2009
Chlamydomonas reinhardtii	Volvocales, Chlorophyta	modern	Domenighini & Giordano 2009
Chlorella marina	Chlorellales, Chlorophyta	modern	Domenighini & Giordano 2009

tabulates the changing diversity of acritarchs and other plausible fungal megafossils as a proxy for evolutionary radiations in Precambrian fungi.

Acritarchs, like many palynomorphs, are an acknowledged taxonomic wastebasket for spheroidal organic-walled microfossils of unknown affinities (Grey 2005). Suggested affinities of acritarchs include Dinoflagellata, Prasinophyceae, Chlorophyceae, Fungi, Mesomycetozoa, and Metazoa. Dinoflagellates, prasinophytes and chlorophytes are aquatic eukaryotic phytoplankton (Moczydłowska et al. 2011). Fungi are marine and terrestrial, eukaroytic decomposers, and include acritarch-like structures in Glomeromycota, orders Glomales (mycorrhizae: Wu et al. 1995), and Archaeosporales (*Geosiphon*: Schüßler 2012), and Mucoromycotina (classification of Hibbett et al. 2007), Order Mucorales (molds: Pereyra et al. 2006). Mesomycetozoa are mostly fish parasites, but include spores with palintomic clusters of cells deceptively similar to animal embryos (Huldtgren et al. 2011). Choanoflagellates and arthropods, produce acritarch-like diapause cysts around embryos with cell differentiation (Cohen et al. 2009). This review suggests that some acritarchs were fungi, but other acritarchs were probably algae, mesomycetozoans and metazoans. As for palynological identifications, distinctive criteria are needed, and several are suggested here.

DIAGNOSTIC FUNGAL FEATURES

The following features are considered diagnostic of fungi, as opposed to algae, Mesomycetozoa or Metazoa, and may constrain their geological antiquity in the fossil record.

Hyphal attachment

A distinctive feature of fungal chlamydospores are attached tubular structures (hyphae) much longer than surficial spines or other ornament (Fig. 1: A–D). *Tappania plana* (Javaux et al. 2001) has the geologically oldest example of such features (at 1466 ± 18 Ma). Such features are also characteristic of acritarch form-genera, such as *Ceratosphaeridium* (Fig. 1 E), whose name implies that this structure is a single oversize "horn" (Grey 2005), in other words, an unusual element of ornament. These elongate elements are hollow and open into the interior of the vesicle (Fig. 1 E,1: G H), so they are not surficial elaborations of the wall. Nor do they appear to be tubular structures spearing the vesicle, as suggested by Cavalier-Smith (2006), because they flare into the outer walls. The form-generic name *Germinosphaera* (Fig. 1 H) implies that the tubular feature was a germination tube, but that is an unlikely explanation given the comparable thickness and cutinization of walls of both the narrow tube and the large spherical body of the vesicle.

These long filaments of comparable materials to the spherical vesicle are similar to hyphae of Glomeromycotan spores, saccules and vesicles (Wu et al. 1995, Walker et al., 2004, Sieverding & Oehl 2006, Pereyra et al. 2006, Schüßler 2012). Similar basal tubular strucutres and wall extensions are also found in the 2200 Ma problematicum *Diskagma* (Retallack et al. 2013 a). Neither algae, mesomycetozoans, nor metazoans emerging from encystment construct single thick-walled tubes markedly narrower than the cyst (Cohen et al. 2009, Huldtgren et al. 2011).

Hyphal fusion

Sparsely septate hyphae which loop and fuse beyond the vesicle wall are best documented in palynomorphs of *Tappania* sp. (Butterfield 2005), which has the geologically oldest known examples of this feature (at 820 ± 10 Ma). These hyphae form a three dimensional net around the vesicle from amalgamation of hyphae diverging at high angles to loop back toward the vesicle: open loops and unfused branches have been interpreted as an unfinished process of hyphal fusion and elaboration (Butterfield 2005).

Hyphal fusion of sparsely septate hyphae is not evidence of higher fungi (Dikarya = Ascomycota + Basidiomycota), as once thought by Butterfield (2005), because it has also been reported in Glomeromycota (Bever & Wang 2005). Hyphal fusion is also found in Oomycota, which are no longer regarded as Fungi, but as Heterokonta (Cavalier-Smith 2006). Cell fusion is also known in vegetative cells of red and brown algae (Porter 2006) and pollen tubes of land plants (Berbee & Taylor 2010).

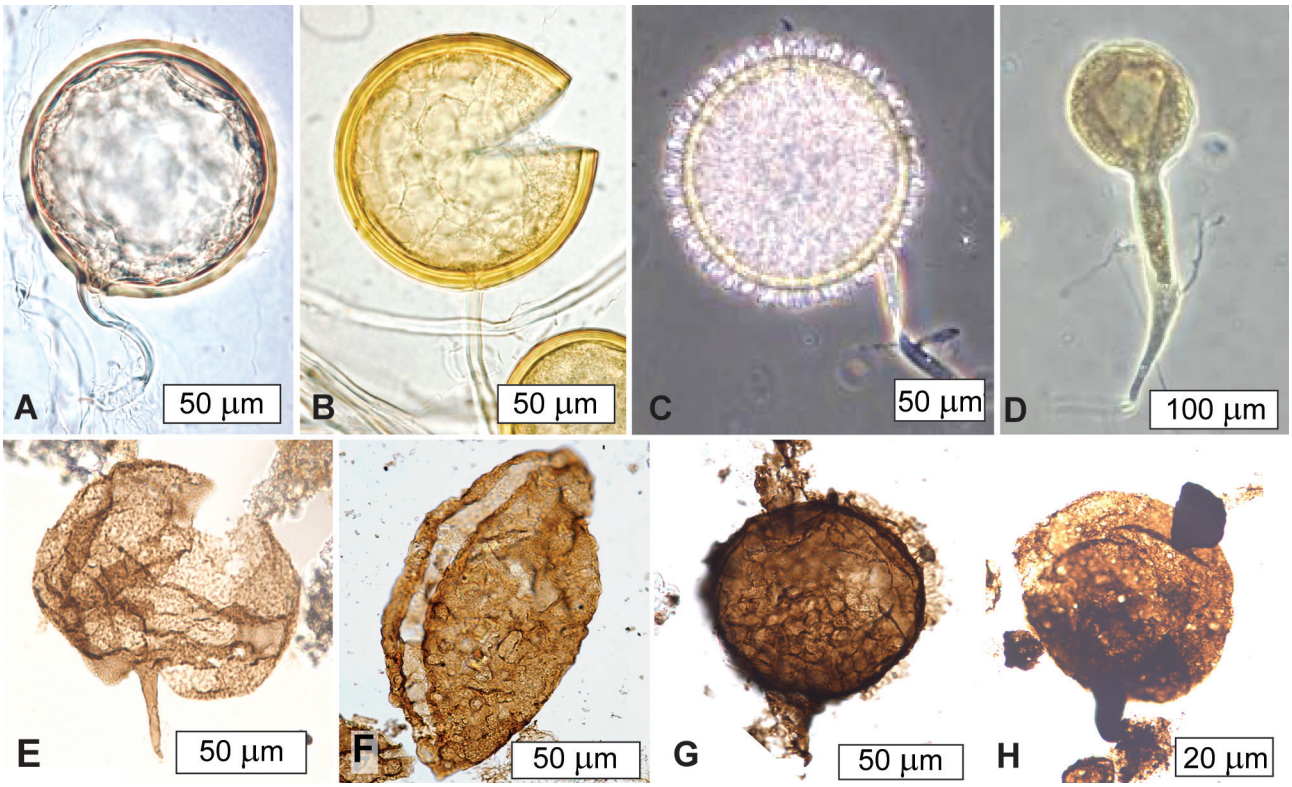

Figure 1 Modern fungal spores (A–C) and sporiferous saccule (D) and comparable Ediacaran acritarchs (E–H): (A) *Glomus claroideum*, Laukan, Finland: (B) *Glomus intraradices*, Îles de la Madeleine, Quebec, Canada: (C) *Gerdemannia chimonobambusae*, Nan-Tou, Taiwan (Wu et al. 1995; Walker et al. 2004); (D) *Acaulospora kentinensis*, Ping-tong, Taiwan (Wu et al. 2005; Sieverding & Oehl 2006; Kaonongbua et al. 2010); (E) *Ceratosphaeridium mirabile*, Wilari Dolomite Member, Tanana Formation, Observatory Hill no., 1 well, northern South Australia (Grey 2005); (F) *Schizofusa zangwenlongii*, Dey Dey Mudstone, Observatory Hill bore, northern South Australia (Grey 2005); (G) *Appendisphaera centroreticulata*, Tanana Formation, Munta 1 bore, northern South Australia (Grey 2005); (H) *Germinosphaera* sp. indet. ABC Range Quartzite, SCYW1a bore, South Australia (Grey 2005): (A–B) by Yolande Dalpé, (C–D) by Chiguang Wu, and (E–H) by K. Grey, with permission

Bulbous wall protrusions

Bulbous wall protrusions are common on vesicles of *Tappania* (Javaux et al. 2001, Butterfield 2005). They are not walls of foreign invading cells such as mycoparasites (Taylor & Osborn 1996), because TEM imaging of protrusions in *Tappania* (Javaux et al. 2004), *Leiospheridia* and *Gyalosphaeridium* (Willman 2009), shows that they balloon out of the internal cavity, and share walls with the same ultrastructural layers, rather than forming callus or reaction tissue.

Javaux et al. (2001) suggested that these wall protrusions were a form of vegetative propagation by budding, implying a protistan affinity. But both walls and spherical protrusions are invested in an acid-resistant biopolymer wall similar to that of the larger structure from which they emerge (Javaux et al. 2004). This kind of wall and arrangement is comparable with vesicles and saccules in Glomeromycotan fungi (Stürmer & Morton 1999).

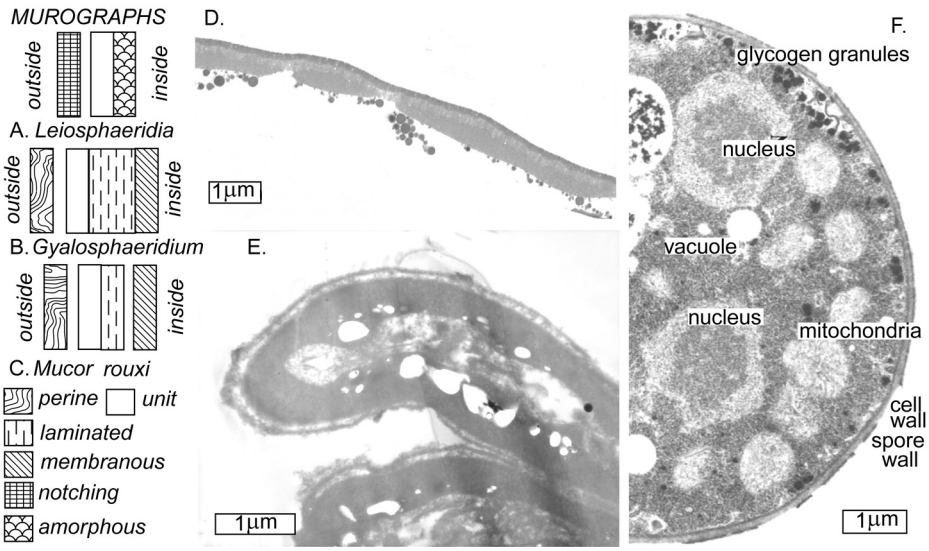

Figure 2 Murographs (A–C) and TEM sections (D–F) of Ediacaran acritarchs (D–E) and a modern fungal spore (F): (A, D) *Leiosphaeridia* sp indet., from Dey Dey Mudstone (Ediacaran), Murnarnoo borehole, northern South Australia (Willman 2009); (B, E) *Gyalosphaeridium pulchrum*, same locality as (A, D) (Willman 2009): (C, F, *Mucor rouxii* sporangiophore (Pereyra et al. 2006). Images courtesy of S. Willman (D–E) and E. Pereyra (F), with permission. Murographs follow conventions of Walker (1983)

Brittle fracture

Elongate sharp slits are characteristic of large smooth acritarchs such as *Leiosphaeridia* and *Schizofusa* (Fig. 1 F), and the oldest known example at 820 ± 10 Ma is *Tappania* sp. (Butterfield 2005, Fig. 1 A). These were not broken during laboratory maceration and mounting of the specimens, because the edges of the splits in the fossils had their outlines thinned and pitted by bacterial decay and framboid growth, which predated burial carbonization (Fig. 1 F). These features are at one end of a spectrum of decay, or taphonomic series, documented for Ediacaran acritarchs by Grey & Willman (2009).

These observations and the elongate sharp slits are evidence of walls that were brittle and tough like chitin, rather than pliable and crushable like cell walls of algal cellulose and algenan. Modern spores of *Glomus* show comparable breakage with pressure on the cover slip, often deliberately applied to reveal this diagnostic frangibility of wall layers (Fig. 1 B).

Multilayered walls

Some acritarchs examined by TEM (Fig. 2: D–E) and as old as 580 ± 4 Ma have a three-layer wall: (1) outermost thin and very electron-dense layer, (2) central electron-tenuous layer, and (3) inner thick moderately electron-dense layer (Willman 2009, Moczydłowska et al. 2010). Wall differentiation is also demonstrated by wrinkling and pulling away of the innermost from the outer walls of some acritarchs (Grey & Willman 2009). Geologically older vesicles examined by TEM do not show differentiated layers (Javaux et al. 2010).

Multilayered vesicle walls are comparable with spore walls of Glomeromycota (Koske & Walker 1986, Koske & Gemma 1995), and cyst walls of Mesomycetozoa (Pekkarinen et al. 2003) and Metazoa (Cohen et al. 2009). Separation and folding of an inner membranous wall in Ediacaran acritarchs (Grey & Willman 2009) is also characteristic of Glomalean fungal spores (Fig. 1 A). Multiple layers of mesomycetozoan and metazoan cyst walls are not separable (Cohen et al. 2009). Algal and Paleozoic acritarchs are quite different under TEM (Talyzina & Moczydłowska 2000), showing radial pores within a thick wall (*Tasmanites*), or homogeneous cell walls (*Comasphaeridium*, *Globosphaeridium*, *Skiagia*).

Walker (1983) proposed a system of murographs for description of glomalean fungal walls, and this system has been applied to two fossil acritarchs and one modern spore in Fig. 2. The murograph of the Ediacaran acritarch *Leiosphaeridia* sp. (Fig. 2 A) is similar to that the living glomalean fungus *Scutellospora hawaiiensis* (Koske & Gemma 1995), although the fossil inner wall has been effaced in patches. The murograph of *Gyalosphaeridium pulchrum* (Fig. 2 B) is more typical of glomalean fungi, such as *Glomus globiferum* (Koske & Walker 1986) and *G. macrocarpum* (Bonfante-Fasolo & Schubert 1987) and archaeosporalean fungi, such as *Geosiphon pyriformis* (Schüßler et al. 1994).

DIAGNOSTIC FUNGAL-ANIMAL FEATURES

The following features distinguish microfossils from algae, but not Mesomycetozoa and Metazoa. A simplified phyletic distribution of these characters is shown in Fig. 3.

Chitin composition

Ediacaran acritarchs as ancient as 580 ± 4 Ma show FTIR spectra (Figs 4: A–D) that closely match chitin and chitosan (Figs. 4: G–M), with 5 characteristic absorption bands (Wu et al. 2005): at wave numbers 3400–3480, 2900, 1650, 1557, 1370 cm^{-1}. Chitosan is deacetylated chitin, produced industrially by leaching with NaOH, but also produced by fermentation with bacteria (Rao & Stevens 2005). This is an appealing explanation for the chitosan composition of some Ediacaran acritarchs, because they also show local dissolution, framboids and shredding comparable with bacterial degradation (Grey & Willman 2009).

Only one of the five FTIR absorption bands for chitin and chitosan is found in fossil algae (*Botryococcus* and *Tasmanites*, Fig. 4: E–F) and only two of these bands are found in modern Oomycota (Helbert et al. 1997), and algae (Fig. 4: N–Q). Chitin has been reported from chlorophyte algae such as *Chlorella* (Němcová 2003), bacillariophytes such as *Thalassiosira* (McLachlan et al. 1965) and chrysophytes such as *Poteriochromas* (Herth et al. 1977), but it is a minor component of the wall in microfibrils within a matrix of cellulose, which would add noise to FTIR spectra. There is genomic evidence that chitin microfibrils in algae are produced by phycoadnaviral infection (van Etten & Meints 1999, Kawasaki et al. 2002, Ali et al. 2007). Chitin and chitosan are widespread and dominate cell walls of fungi, including Chytridiomycota, Glomeromycota, Basidiomycota and Ascomycota (Bartnicki-Garcia 1968, Wu et al. 2005, Kaminskyj et al. 2008, Calderón et al. 2009), as well as exoskeletons of arthropods (Sini et al. 2007, Matján et al. 2007).

NON-DIAGNOSTIC FEATURES

The following features have been regarded as benchmarks in acritarch evolution, but are too widespread or uncertain to be distinctive of particular clades.

Large size

Unusually large size is a feature of Ediacaran acritarchs permissive of fungal affinities, but shared by mesomycetozoan and metazoan cysts (Cohen et al. 2009, Huldtgren et al. 2011), algal phycomata (Colbath 1983), giant sulphur bacteria such as *Thiomargarita namibiense* (Bailey et al. 2007), and actinobacteria such as *Amycolatopsis decaplanina* (Cavalier-Smith 2006). Most Phanerozoic acritarchs and modern unicellular algae are 20–50 μm in diameter, whereas Precambrian smooth and spiny acritarchs range in size from 20–500 μm in diameter, with a modal diameter of 220 μm (Cohen et al. 2009).

Cell inclusions

Also permissive of fungal-holozoan-metazoan affinities are inclusions within Ediacaran acritarchs. Electron-dense granules seen inside some Ediacaran acritarch walls (Fig. 2 E) are comparable with glycogen granules, and other inclusions (Fig. 2 E) are similar to nuclei and mitochondria of Glomeromycota (Fig. 2F). Large internal bodies with accommodating sides in Mesomycetozoa (Pekkarinen et al. 2003, Huldtgren et al. 2011) are morphologically similar to an early (morula) stage of metazoan embryonic de-

velopment. Comparable internal contents within the Ediacaran acritarch *Tianzhushania*, have never been found beyond what would be a morula stage of a metazoan (Xiao et al. 2012, Schiffbauer et al. 2012, Yin et al. 2013).

Surface ornament

Spiny outer surfaces do not exclude fungal affinities, and are common in all the organisms under consideration (Arouri et al. 1999, 2000, Cohen et al. 2009, Moczydłowska et al. 2011, Yin et al. 2013). Many spores of Glomeromycota are smooth, but not all: spiny acritarchs such as *Appendisphaera* (Fig. 1 G) are comparable with spores of Glomalean fungi such as *Gerdemannia* (Fig. 1 C).

PRECAMBRIAN FUNGAL BENCHMARKS

The various fungal features discussed can be used to reassess specific occurrences as potential benchmarks in the palynological record of fungi: specifically 1466 ± 18 Ma minimum age of Glomeromycota, and 599 ± 4 Ma appearance of lichenized Mucoromycotina. Despite claims of Butterfield (2005) and Schopf & Barghoon (1969) for evidence of Precambrian higher fungi (Ascomycota and Basidiomycota), these clades are not convincingly represented by Precambrian palynomorphs (Strother et al. 2011), and remain unknown older than Silurian (Sherwood-Pike & Gray 1985, Taylor & Osborn 1986, Burgess & Edwards 1991, Taylor & Taylor 2000, Taylor et al. 1997, 2005, 2014, Honegger et al. 2013, Matsunaga et al. 2013).

1466 ± 18 Ma and 820 ± 10 Ma Glomeromycota

Tappania plana from the 1466 Ma Roper River Group of Northern Territory has the following fungal features: irregular polyhedral-spherical shape, large size (up to 160 μm), spherical cell wall protrusions, and hyphal attachment (Javaux et al. 2001). The palynomorphs show what appears to be several wall layers, but TEM examination of a very deformed specimen showed little detail and was interpreted as massive (Javaux et al. 2004). *Tappania* sp. indet. from the 820 Ma Wyniatt Formation of Nunavut has in addition elongate and lobate shapes, rhizine-like attachments, fused hyphae, and sizes up to 300 μm long (Butterfield 2005).

Tappania from the shallow marine facies of the lower Corcoran Formation and shoreface facies of the upper Jalboi Formation of the Roper River Group in the McArthur Basin, Northern Territory (Javaux et al. 2010) is bracketed by a U-Pb SHRIMP zircon age of 1492 ± 4 Ma from an ash bed below, and an Rb-Sr isochron age of for 1429 ± 31 Ma on illite in dolomitic siltstones near the top of the succession (Kralik 1982, Page et al. 2000). Interpolating between these ages and errors gives 1466 ± 18 Ma for the fossiliferous levels.

A more varied suite of *Tappania* and similar *Germinosphaera* fossils from shallow marine shales of the lower Wynniatt Formation, on Victoria Island, Nunavut (Butterfield 2005), is associated with cyanobacterial microfossils as evidence of deposition within the photic zone (Butterfield & Rainbird 1998). The lower Wynniatt Formation is older than Franklin diabase intrusions dated by U/Pb on baddeleyite at 716.33 ± 0.54 Ma (MacDonald et al. 2010), and younger than detrital zircons from sandstone dated by U-Pb at 1077 ± 4 Ma (Rainbird et al. 1996). Wynniatt Formation carbon isotopic data is evidence of an age immediately before (only 20 m below) the onset of the Bitter Springs anomaly, which in turn is dated by U/Pb on zircons in a tuff at 811.5 ± 0.25 Ma in the Ogilvie Mountains of northwest Canada (MacDonald et al. 2010). Chemostratigraphic correlation gives an age of 820 ± 10 Ma for the lower Wynniatt Formation (Jones et al. 2010).

In retrospect it is surprising that *Tappania* was included within acritarchs, which are more regularly spherical and have sharply ending, and radially arranged processes (Moczydłowska et al. 2011). Fusion of sparsely septate hyphae is not evidence of higher fungi (Ascomycota + Basidiomycota), as once thought (Butterfield 2005), because hyphal fusion and septae are now known in Glomeromycota (Bever & Wang 2005), as well as Oomycota, algae and Plantae (Porter 2006, Berbee & Taylor 2010). Considered in this new light, *Tappania* may be compared with saccules of extant *Acaulospora kentinensis* (Fig. 1 D), spores of extant *Gerdemannia chimonobambusae* (Fig. 1 C), and fungal sclerotia (Moore 2013). Unlike these living taxa, it was not mycorrhizal with land plants, and did not show germination shields. *Tappania* is covered in hyphae unlike glomalean spores (Pirozynski & Dalpé 1989) and the endosymbiotic bladders of the glomeromycotan *Geosiphon* (Schüßler 2012). *Tappania* also appears hollow, unlike sclerotia (Moore 2013). It is here regarded as a glomeromycotan saccule.

Fungal affinities of *Tappania* have been disputed. Cavalier-Smith (2006) compared *Tappania* with actinobacterial pseudosporangia like those of living *Amycolatopsis decaplanina*, while admitting that actinobacteria are smaller and less complex. Porter (2006) and Berbee & Taylor (2010) noted that cell fusion is also found in vegetative cells of red and brown algae, between antheridia and oogonia of Oomycota, and pollen tube and embryo sac in plants, but these are not fused septate hyphae. Porter (2006) and Javaux (2007) also questioned whether the Wynniatt Formation material could be referred to *Tappania*, because hyphal fusion was not illustrated in holotypes of *Tappania* from the Beidajian Formation by Yin (1997). The holotypes had short broken hyphae, known to be a consequence of rough treatment during preparation, but even if the name is incorrect, that does not falsify the observed features (Butterfield 2005). Berbee & Taylor (2010) found similarities between the hyphal mesh of *Tappania* and fungal adaptations for animal dispersal, but the neatness of the mesh in some specimens is also a taphonomic-preparation artefact, as shown by more ragged examples (Butterfield 2005), including rhizine-like extensions (Butterfield 2005: grading into "*Germinosphaera*"). Rhizine-like structures are significant because Berbee & Taylor (2010) mistakenly assumed they were lacking. The statement of Moczydłowska et al. (2011) that "Fungal spores have no morphologically complex processes like …. acritarch genera", is also untrue (Fig. 1: C–D). Moczydłowska et al. (2011) also consider collar-like extensions of the wall of *Tappania* to be algal excystment structures, rather than fungal hyphae or rhizines, but excystment structures are not collars, but slits, often defining an operculum, as demonstrated by fossil (Yuan et al. 2001) and living microbes (Bowers & Korn 1969).

599 ± 4 Ma cyanolichen

An un-named permineralized cyanolichen from the Doushantuo Formation near Weng'an, China, has been reported from bituminous phosporites (Yuan et al. 2005). The phosphorite has been dated by several methods, the most precise based on U-Pb on apatite from the fossil bed yielded an age of 599.2 ± 4.3 Ma (Barfod et al. 2002). This date is supported by additional bracketing dates of Condon et al. (2005).

This fossil is a lichenlike association of phosphate-permineralized branching hyphae with terminal saccules or spores intimately associated with coccoid cells, and has been interpreted as a mucoromycotan host to cyanobacterial photobiont by Yuan et al. (2005). Such close association of mycobiont and phycobiont is typical of ascolichens and basidiolichens (Honegger et al. 2013, Matsunaga et al. 2013), but unknown in any living Glomeromycota or Mucromycotina, and so represents an extinct clade of ectolichens. The only extant symbiotic glomeromycotans are endocyanotic *Geosiphon* (Schüßler 2012), and such endosymbiosis is not accepted as a true "lichen" in some quarters (Hawksworth & Honegger 1994).

The Weng'an lichen fossil has been assumed to have been marine like associated fossil algae (Xiao et al. 2004) and mesomycetozoans (Huldtgren et al. 2011), but recent mineralogical study suggests that the Doushantuo Formation was deposited in a lake (Bristow et al. 2009). Furthermore the fossil is a rare small fragment only 0.5–5 m stratigraphically above a paleokarst (Yuan et al. 2005). More complete remains are needed, and presumably available from this well sampled locality (Bengtson et al. 2012), to determine whether this fossil was aquatic or terrestrial.

583 ± 2.3 Ma brittle multilayered chitin walls

Leiosphaeridia sp. indet. and *Gyalosphaeridium pulchrum* from the Dey Dey Mudstone at 230.4 m in Murnarnoo borehole of northern South Australia are not only large (150–400 and 350–450 μm diameter respectively) but have a chitin composition, brittle fracture, and at least three wall layers (Willman & Moczydłowska 2007, Willman 2009). The Dey Dey Mudstone includes dropped pebbles as evidence for glaciation which Gostin et al. (2010) correlate with Gaskiers Glaciation, which in turn is dated by U-Pb analysis of zircons in Newfoundland as 582.4 ± 0.5 Ma to 583.7 ± 0.5 Ma (van Kranendonk et al. 2008). The Dey Dey Mudstone in nearby boreholes (Munta 1 and Observatory Hill 1) also includes the global Shuram-Wonoka carbon isotopic excursion, correlated by Halverson et al. (2010) and Le Guerroué (2010) with the Gaskiers Glaciation, but better correlated with end of the Fauquier Glaciation with interpolated age of 567 ± 6 Ma (Retallack et al. 2014). These acritarchs are not unusual for Ediacaran palynomorphs, but have been studied in more detail by TEM and FTIR than most to reveal characteristic fungal features. Additional studies are needed to establish fungal affinities of other acritarchs.

ACRITARCH DIVERSIFICATION RECONSIDERED

Diversification then decline of the Ediacaran Complex Acanthomorph Palynoflora (ECAP acritarchs) is a remarkable Late Ediacaran biological event (Schopf 1999, Grey, 2005), coincident with rise and decline of the enigmatic Vendobionta (Fig. 5, Table 2). After acritarch and vendobiont mass extinctions at the Cambrian-Precambrian boundary, a diversification of unrelated small acritarchs (Talyzina & Moczydłowska 2000, Moczydłowska et al. 2011) accompanied the Cambrian explosion of metazoa and metaphytes (Fedonkin et al. 2008, Erwin et al. 2011).

Ediacaran diversification of large acritarchs has been attributed to metazoan diversification, based on interpretation of Vendobionta as metazoans, a limited array of putative metazoan trace fossils, and putative permineralized metazoans and embryos (Gaucher & Sprechmann 2009, Cohen et al. 2009, Erwin et al. 2011). However, evidence for Ediacaran metazoans is dwindling. A combination of simple morphology and indifferent preservation of most soft-bodied Ediacaran and Cryogenian fossils has compounded the mystery: none can be unequivocally attributed to metazoans (Antcliffe & Brasier 2008, Antcliffe et al. 2011, Erwin et al. 2011, Meert et al. 2011). Some of these

Table 2. Vendobiont generic diversity curve

Assemblage	Age	Ma	Genera	Reference
Grindstone Range, South Australia, Australia	early Early Ordovician	482–488	4	Retallack 2009
Mosinee, Wisconsin, USA	Late Cambrian	488–501	1	Hagadorn et al. 2002
Booley Bay, Ireland	late Middle Cambrian	501–505	2	Vanguestaine & Brück 2005
Burgess Shale, British Columbia, Canada	early Middle Cambrian	505–513	1	Conway Morris 1993
Death Valley, California, USA	late Early Cambrian	513–515	1	Hagadorn et al. 2000
Chengjiang, Yunnan, China	middle Early Cambrian	515–525	1	Shu et al. 2005
Mudlapena Gap, South Australia, Australia	early Early Cambrian	525–542	2	Jensen et al. 1998
Nama, Namibia	late late Ediacaran	542–550	15	Shen et al. 2008
Ediacara Hills, South Australia, Australia	late Ediacaran	550–555	77	Shen et al. 2008
Ferryland, Newfoundland, Canada	late Ediacaran	555–560	7	Gehling et al. 2000
Mistaken Point, Newfoundland, Canada	middle Ediacaran	560–570	30	Wilby et al. 2011
Ives Head, Leicestershire, England	early middle Ediacaran	570–600	5	Boynton & Carney 2003
Bunyeroo Gorge, South Australia, Australia	early Ediacaran	600–635	1	Runnegar & Fedonkin 1991
Mount Remarkable, South Australia, Australia	late Cryogenian	635–700	1	Runnegar & Fedonkin 1991
Lualobei, Anhui, China	middle Cryogenian	700–850	1	Sun et al. 1986; Meert et al. 2011

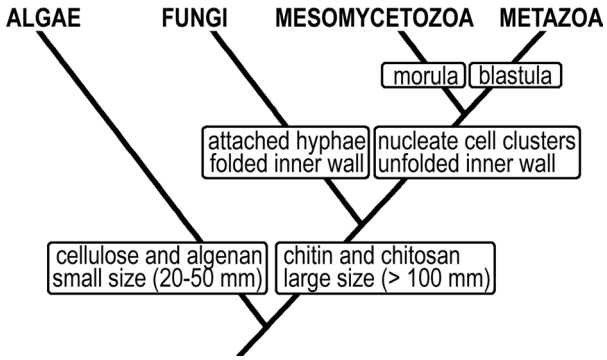

Figure 3 Diagnostic biological features of acritarchs on a simplified phyletic tree

unskeletonized Ediacaran organisms lived on dry land (Retallack 2013 a). Skeletonized and phosphatic Cryogenian and Ediacaran fossils including *Cloudina* and *Corumbella* are more convincing as animals, but difficult to assign to modern animal groups (Fedonkin et al. 2008, Maloof et al. 2010). Non-penetrative trace fossils (Pecoits et al. 2012, Chen et al. 2013) could have been the work of slug-aggregating phases of amoeboid organisms, such as slime molds (Bengtson et al. 2007, Retallack 2012, 2013b). In other cases, supposed trails (Liu et al. 2010a, 2010b) appear to be tool marks (Retallack 2010). Supposed Ediacaran animal embryos in acritarchs from the Doushantou Formation at Weng'an may have been giant sulfur bacteria (Bailey et al. 2007) or mesomycetozoans (Huldtgren et al. 2011), rather than metazoans. Although the embryo interpretation remains defensible with contraindications explained by taphonomic artefacts (Xiao et al. 2012, Schiffbauer et al. 2012, Yin et al. 2013), there has not yet been found a convincing Ediacaran embryo like those from Cambrian phosphorites (Zhang et al. 2011). A putative permineralized metazoan ("*Vernanimalcula guizhouensis*") also from Weng'an appears to be mineralized vugs (Bengtson et al. 2012, Petryshyn et al. 2013). This leaves only biomarker (Love et al. 2009) and skeletal (Maloof et al. 2010) evidence for Cryogenian (635–713 Ma) organisms of sponge grade. Gemmules of sponges, listed as plausible acritarchs by Cohen et al. (2009), are spiculate fossils (Harrison & Warner 1986), unlike most Precambrian acritarchs.

Ediacaran diversification of large acritarchs (Fig. 5 C) and Vendobionta (Fig. 5 B) may reflect mostly diversification of Glomeromycota and Mucoromycotina, rather than giant sulfur bacteria, Mesomycetozoa or Metazoa. Cambrian diversification of small spiny acritarchs of modern appearance, on the other hand, may represent the rise of phytoplankton and metazoan resting phases (Cohen et al. 2009, Moczydłowska et al. 2011) fuelling the Cambrian explosion of small shelly fossils and most modern marine invertebrate phyla (Erwin et al. 2011). Acritarchs were diverse, like other palynomorphs, and a simplified guide to their affinities is presented in Fig. 3. By all likely affinities Proterozoic acritarchs were broadcast propagules, like other palynomorphs, finding their way from, and into, marine, freshwater and terrestrial habitats (Strother et al. 2011). Proterozoic acritarchs like vendobionts (Retallack 2013a, 2014) can no longer be assumed to have been entirely marine.

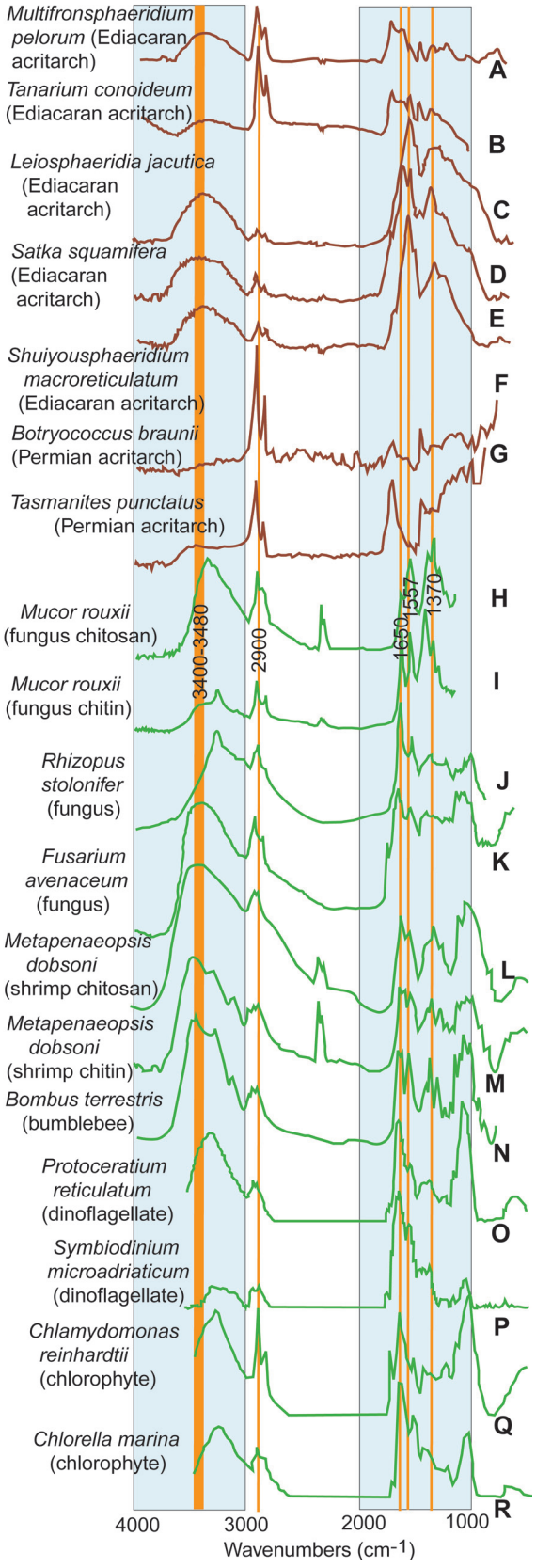

Figure 4 FTIR spectra of acritarchs (A–F) and a range of comparable modern organisms (G–Q). Ediacaran acritarchs (A–D) have spectra comparable with chitin and chitosan of fungi, shrimp and bees (H–N), distinct from the composition of Paleozoic acritarchs (E–F) and modern phytoplankton (O–Q). Vertical lines are characteristic chitin and chitosan absorption bands (Wu et al 2005) at 1370, 1557, 1650, 2900 and 3400–3480 cm^{-1}. Sources of spectra are in Table 1

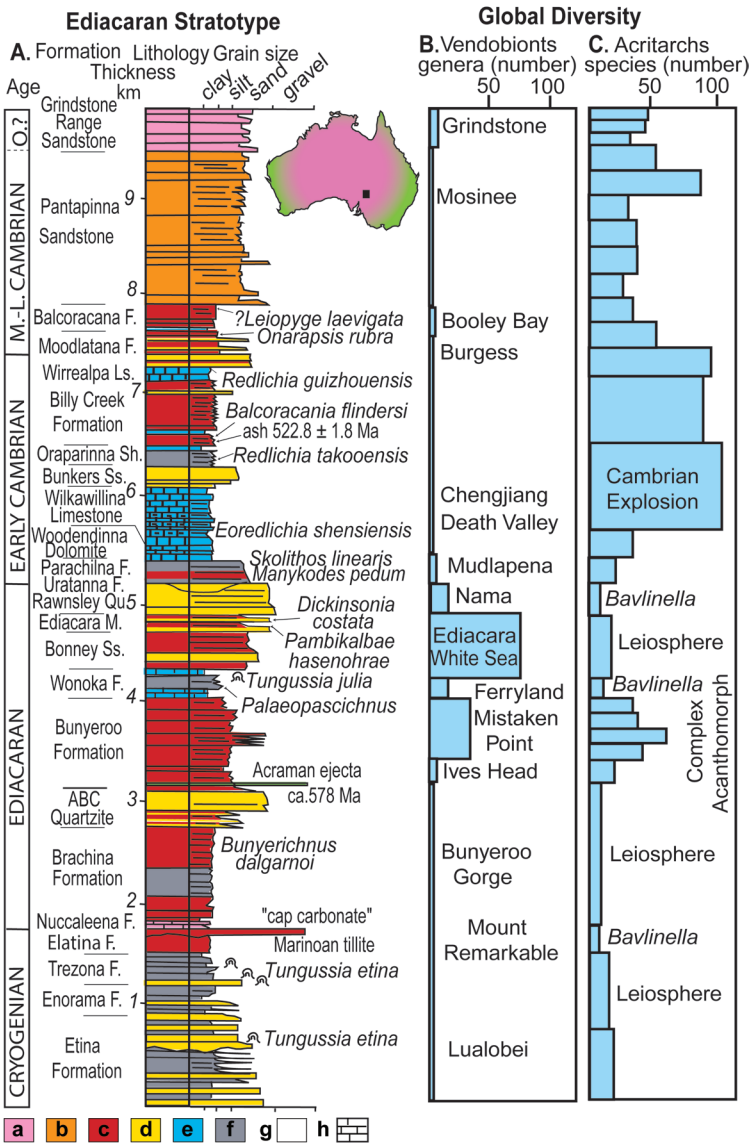

Figure 5 Ediacaran stratotype section in South Australia (A) and global diversity of Vendobionta (B) and acritarchs (C) (see Tables 2 and 3 for sources). Lithological groups: a – pink sandstone, b – red sandstone, c – red siltstone, d – white sandstone, e – light-gray limestone, f – dark-gray shale, g – clastic, h – carbonate

Acritarchs regarded here as records of Mesoproterozoic Glomeromycota agree with a fungal molecular clock pushing the fungus-animal split back 2200 Ma based on nucleotide substitution of 50 genes (Taylor & Berbee 2006), pegged to the sordariomycete ascomycotan *Paleopyrenomycites devonicus* from the early Devonian Rhynie Chert of Scotland (Taylor et al. 2005). This clock is compatible with the likely Archaeosporalean glomeromycotan *Diskagma buttonii* from the 2200 Ma Waterval Onder paleosol of South Africa (Retallack et al. 2013a), probable siphoneous green algae *Grypania spiralis* from the 1874 Ma Negaunee Iron Formation of Michigan (Han & Runnegar 1991, Schneider et al. 2002), the first appearance of trilobites at 521 Ma (Hollingsworth 2008) and well preserved glomeromycotan spores at 449 Ma (Redecker et al. 2000). Other molecular clocks have the fungus-animal spit at about 1600 Ma (Heckman et al. 2001, Bhattacharya et al. 2009), 1200–820 Ma (Lücking et al. 2009) and 950 Ma (Berbee & Taylor 2010). Molecular clock ages remain uncertain, but all trees cited here demonstrate an early divergence of Glomeromycota and Mucoromycotina, well before Basidiomycota and Ascomycota. The lack of ascospores and basidiospores in Precambrian palynological preparations is striking (Strother et al. 2011). A plausible ascus from the 790 Ma Skillogalee Dolomite of South Australia (Schopf & Barhgoorn 1969, Preiss et al. 2009) has been reinterpreted as an intercalary oogonium of a water mold (Saprolegniales, Oomycota) by Pirozynski (1976).

MYCOTROPHIC HYPOTHESIS EMENDED

The hypothesis presented here of diverse Ediacaran Glomeromycota has implications for the mycotrophic ("fungal feeding") hypothesis of Jeffrey (1962). The mycotrophic hypothesis was more fully fleshed out by Pirozynski & Malloch (1975), who proposed that plant colonization of land required nutrition from fungal mycorrhizae. Glomalean fungi of the phylum Glomeromycota are essential for nutrient acquisition on land as mycorrhizal symbionts of most vascular land plants (Malloch et al. 1980, Wang & Qiu 2006), and many bryophytes (Ligrone et al. 2007). Two minor aspects of their original hypothesis are now problematic. First, Pirozynski & Malloch (1975) argued that Oomycota were the essential fungal partner, but mycorrhizal fungi (Glomales, Glomeromycota: Hibbett et al. 2007) have now been segregated from Oomycota (water molds, such as *Phytophora cinnamoni*), which are not Fungi, but Heterokonta (Cavalier-Smith 2006). Second, Pirozynski & Malloch (1975) and Jeffrey (1962) both linked their hypothesis to the idea that multicellular aquatic green algae colonized the land. Stebbins & Hill (1980) have argued that archegoniate land plants evolved from fully terrestrial small soil algae, with three dimensional thalli and conjugation rather than zoospores. Conjugation and fungal mycotrophism are more effective on land than in water (Hawksworth 2000), and this is accepted here as a useful amendment to the mycotrophic hypothesis. With these caveats, the core concept of the mycotrophic hypothesis that land was prepared for plants by fungi is now supported by likely Proterozoic glomeromycotan-mucoromycotan acritarchs (Figs. 1–4) and other fossils (Retallack et al. 2013a, 2013b), and a Paleozoic fossil record of Glomalean fungi before land plants (Pirozynski 1976, Pirozynski & Dalpé 1989, Redecker et al. 2000). *Diskagma* (Retallack et al. 2013a), *Horodyskia* (Retallack et al. 2013b), and *Tappania* (Butterfield 2005) may have been free-living glomeromycotans in loose association with cyanobacterial mats, predicted as hypothetical organisms by Sherwood-Pike (1991).

Four other lines of support for the mycotrophic hypothesis also postdate its elaboration by Pirozynski & Malloch (1975). First, Archaeosporales are a group of free living soil

Table 3. Acritarch specific diversity curve

Acritarch assemblages	Age	Ma	Spp.	Reference
Cymatiogalea messaoudensis	early Migneintan	482-484	49	Vecoli & Le Hérissé 2004
Cymatiogalea messaoudensis	late Cressagian	484-488	48	Vecoli & Le Hérissé 2004
Acanthodiacrodium angustum	early Cressagian	486-488	37	Vecoli & Le Hérissé 2004
Izhoria angulata	UC6	488-490	54	Vidal & Moczydłowska 1997, Raevskaya 2005
Impluviculus villosiuculus	UC5	490-492	86	Vidal & Moczydłowska 1997, Raevskaya 2005
Trunculumarium revinium	UC4	492-494	30	Vidal & Moczydłowska 1997, Raevskaya 2005
Impluliviculus multiangularis	UC3	494-496	37	Vidal & Moczydłowska 1997, Raevskaya 2005
Cymatiogalea spp.	UC2	496-498	37	Vidal & Moczydłowska 1997, Raevskaya 2005
Timofeevia pentagonalis	UC1	498-501	27	Vidal & Moczydłowska 1997, Raevskaya 2005
Timofeevia phosphoritica	*P. forchammeri*	501-504	33	Vidal & Moczydłowska 1997, Raevskaya 2005
Cristallinium cambriense	*P. paradoxisiumus*	504-507	54	Vidal & Moczydłowska 1997, Raevskaya 2005
Baltisphaeridium pseudofaveolatum	*A. oelandi*	507-510	93	Vidal & Moczydłowska 1997, Raevskaya 2005
Volkovia-Liepania	*Protolenus*	510-512	86	Vidal & Moczydłowska 1997, Raevskaya 2005
Heliosphaeridium-Skiagia	*Holmia igerulfi*	512-525	102	Vidal & Moczydłowska 1997, Raevskaya 2005
Skiagia-Fimbriaglomerella	*Schmidtiella*	525-534	36	Vidal & Moczydłowska 1997, Raevskaya 2005
Asteridium-Compaesphaeridium	*Platysolenites*	534-542	22	Vidal & Moczydłowska 1997, Raevskaya 2005
Bavlinella faveolata (LELP crisis)	Late Ediacaran	542-550	9	Gaucher & Sprechmann 2009
Trachysphaeridium partiale	Late Ediacaran	550-555	14	Leonov & Ragozina 2007
Bavlinella faveolata (LELP crisis)	Late Ediacaran	555-560	9	Gaucher & Sprechmann 2009
Ceratosphaeridium mirabile ECAP	Middle Ediacaran	560-565	30	Grey 2005
Tanarium irregulare (ECAP)	Middle Ediacaran	565-570	32	Grey 2005
Tanarium conoideum (ECAP)	Middle Ediacaran	570-575	48	Grey 2005
Appendisphaera barbata (ECAP)	Middle Ediacaran	575-580	33	Grey 2005
Leiosphaeridia spp. (EELP)	Early Ediacaran	590-610	15	Gaucher & Sprechmann 2009
Leiosphaeridia spp. (EELP)	Early Ediacaran	610-635	11	Gaucher & Sprechmann 2009
Bavlinella faveolata (crisis)	Late Cryogenian	635-675	10	Gaucher & Sprechmann 2009
Papillomembrana-Ericiasphaera	Late Cryogenian	675-700	17	Gaucher & Sprechmann 2009
Papillomembrana-Ericiasphaera	mid-Cryogenisn	700-740	21	Gaucher & Sprechmann 2009
Bavlinella faveolata (crisis)	mid-Cryogenisn	740-765	11	Gaucher & Sprechmann 2009
Simia-Cerebrosphaera	Early Cryogenian	765-820	41	Gaucher & Sprechmann 2009
Simia-Cerebrosphaera	Early Cryogenian	820-840	33	Gaucher & Sprechmann 2009
Simia-Cerebrosphaera	Early Cryogenian	840-930	15	Gaucher & Sprechmann 2009
Simia-Cerebrosphaera	Early Cryogenian	930-1200	11	Gaucher & Sprechmann 2009

glomeromycotans represented by *Geosiphon pyriforme*, which has a large vesicle to contain the endosymbiotic cyanobacterium *Nostoc punctiforme* (Schüßler et al. 1994, Schüßler 2012). Thus not all glomeromycotan fungi are dependent on vascular plant roots.

Second, studies of ecological succession in western North American desert soil crusts show the following stages: 1, bare soil; 2, large filamentous cyanobacteria such as *Microcoleus vaginatus*; 3, gelatinous lichens such as *Collema coccophorum*; 4, squamulose lichens such as *Psora cerebriformis*; 5, crustose lichens such as *Diploschistes scruposus*; 6, liverworts such as *Cephaloziella divaricata*; 7, short mosses such as *Bryum argenteum*; 8, foliose lichens such as *Xanthoparmelia convoluta*; 9, tall mosses such as *Syntrichia ruralis*; 10, fruticose lichens such as *Aspicilia filiformis*; 11, early successional angiosperms such as *Chrysothamnus nauseus*, and 12, late successional angiosperms such as *Artemisia tridentata* (Rosentreter 1984, Belnap et al. 2001). Current ecological succession may be recapitulating Precambrian communities of lichens and microbes on land (Retallack 2012), with cyanobacterial stage 2 reached very early in Earth history, lichen stage 3 by the Proterozoic, non-vascular land plant stage 6 by Ordovician (Katian), and the vascular plant stage 11 by Silurian (Wenlockian: Retallack 2001, Retallack et al. 2013a).

Third, free living lichens, in which cyanobacterial phycobionts are enclosed by glomeromycotan-mucoromycotinan hyphae, are represented by an un-named permineralized fossil from the Doushantou Formation near Weng'an, China (Yuan et al. 2005). Thus glomeromycotan-mucoromycotinan fungi included extinct forms of lichens constructed in a manner comparable with familiar ascolichens and basidiolichens (Honegger et al. 2013, Matsunaga et al. 2013), in addition to likely endosymbiotic forms such as *Diskagma* (Retallack et al. 2013a), and *Horodyskia* (Retallack et al. 2013b).

Fourth, paleosols of Ordovician to Paleoproterozoic ages show evidence of life on land from chemical depletion of phosphorus and cationic nutrients (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}) and filamentous bioturbation comparable with, though less intense than, modern soils (Retallack 2008, 2009, 2011, 2013a, Retallack et al. 2013a). Many of these paleosols were calcareous and fertile, but some were quartzose and infertile substrates (Retallack 2009, 2013a) insufficiently organic to support large populations of unlichenized fungi. Some of these paleosols supported vendobiont fossils with lichenlike features such as indeterminate growth, compaction resistant biopolymers and tubular-fractal construction

(Retallack 2007, 2013a). The Paleoproterozoic (2200 Ma) fossil *Diskagma buttonii* may be the oldest Glomeromycotan fungus, and was found in a Vertisol paleosol formed under a moderately oxidizing atmosphere and cool temperate paleoclimate (Retallack et al. 2013a). Latest Archean (2600 Ma) *Eomycetopsis* may represent even older Glomeromycota from stromatolitic (thus aquatic) cherts (Altermann & Schopf 1995). *Eomycetopsis* is a tubular microfossil named for its close similarity with fungal hyphae (Schopf 1968), but subsequently reinterpreted as cyanobacterial sheaths because aseptate (Knoll 1982). This objection to assigning *Eomycetopsis* to Ascomycota or Basidiomycota does not apply to Glomeromycota, which are mainly aseptate (Hibbett et al. 2007, Moore 2013).

Theories of lichen evolution unsupported by the fossil record include the ascophyte hypothesis of Cain (1972) and the protolichen hypothesis of Eriksson (2005), which both address ascomycotan evolution. Cain (1972) envisaged ascomycotans as fundamentally terrestrial and derived from photosynthetic red algae that lived on land. Eriksson (2005) proposed that higher ascomycotans (*Pezizomycotina*) were derived from lichens rather than saprobes. These views are countered by a recent phylogenetic tree showing that ancestral ascomycotans were saprophytic rather than lichenized or free living (Schoch et al. 2009). Both views are also countered by lack of evidence for ascomycotan fossils older than vascular land plants of Late Silurian age (425 Ma (Sherwood-Pike & Gray 1985, Burgess & Edwards 1991, Taylor et al. 2014). The Early Devonian (400 Ma) Rhynie Chert of Scotland has yielded secure records of saprophytic chytrids and oomycotans, mycoparasitic chytrids, phytoparasitic chytrids and pyrenomycete ascomycotans, glomalean arbuscular endomycorrhizae, and mucoromycotinan lichens (Taylor & Taylor 2000, Taylor et al. 2005, 2014). The Early Devonian Ditton Group of Wales has yielded ascomycotan and basidiomycotan lichens (Honegger et al. 2013).

CONCLUSIONS

Large Proterozoic acritarchs such as *Tappania*, *Leiosphaeridia*, *Gyalosphaeridium*, *Ceratosphaeridium* and *Germinosphaera* (Grey 2005, Butterfield 2005), with hyphae and chitinous multi-layered walls are here regarded as Glomeromycotan fungal chlamydospores and vesicles, confirming glomeromycotan-mucoromycotinan affinities of an un-named Ediacaran permineralized lichen (Yuan et al. 2005), Mesoproterozoic *Horodyskia* (Retallack et al. 2013b) and Paleoproterozoic *Diskagma* (Retallack et al. 2013a). Glomeromycotan, rather than ascomycotan or basidiomycotan, affinities are thus more likely for Ediacaran impression fossils considered fungal, such as *Dickinsonia* (Retallack 2007, 2013) and *Fractifusus* (Peterson et al. 2003, Gehling & Narbonne 2007). Considering lack of unequivocal Ediacaran metazoan fossils (Bengtson et al. 2007, 2012, Huldtgren et al. 2011, Petryshyn et al. 2012), other than sponges which have distinctive gemmules (Harrison & Warner 1986), late Ediacaran diversification of large acritarchs may have been an evolutionary event mainly involving fungi. The Paleoproterozoic appearance of glomeromycotan fungi (Retallack et al. 2013a) also supports a glomeromycotan mycotropic (Pirozynski & Malloch 1975) and terrestrial (Stebbins & Hill 1980) origin of Early Paleozoic land plants. Glomeromycota still secure the nutrition of most land plants as symbiotic mycorrhizal associations (Wang & Qiu 2006), and may have been essential to the nutrition of early land plants and subsequently of primitively saprophytic higher fungi such as Basidiomycota and Ascomycota (Schoch et al. 2009).

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Greg Retallack:

On discovering Valentin Krassilov's marvellous 1977 book "Paleoecology of terrestrial plants", I at first felt scooped, but then overwhelmed at the range of examples and sweep of ideas. In my mind's eye I pictured him as a jocund and rotund senior scientist of vast experience, much nose hair and an ill-fitting suit, like many Russian scientists of the time. To my great surprise on meeting him for the first time at the 1984 International Geological Congress in Moscow, I found that he was little older than me, athletic, very fashionably dressed, and with an attractive young wife. He had an intensity and seriousness of purpose that was fascinating. This was just the beginning of his career, and yet he had already accomplished so much.