Chapter 1

The Proterozoic Fossil Record of Heterotrophic Eukaryotes

SUSANNAH M. PORTER

Department of Earth Science, University of California, Santa Barbara, CA 93106, USA.

1. INTRODUCTION

Nutritional modes of eukaryotes can be divided into two types: autotrophy, where the organism makes its own food via photosynthesis; and heterotrophy, where the organism gets its food from the environment, either by taking up dissolved organics (osmotrophy), or by ingesting particulate organic matter (phagotrophy). Heterotrophs dominate modern eukaryotic

Neoproterozoic Geobiology and Paleobiology, edited by Shuhai Xiao and Alan Jay Kaufman,

diversity, in fact, autotrophy, which characterizes the algae and land plants, appears to be a derived condition, having evolved several times within the eukaryotes (e.g., Keeling, 2004; although see Andersson and Roger, 2002). Indeed, heterotrophy is a *prerequisite* for autotrophy in eukaryotes, as the plastid – the site of photosynthesis in eukaryotes -- was originally acquired via the ingestion of a photosynthetic organism. Thus it may be surprising that the early fossil record of eukaryotes is dominated not by heterotrophs but by algae. Most of the fossils that can be assigned to a modern clade are algal (red, xanthophyte, green, or brown; German, 1981, 1990; Butterfield *et al*., 1990, 1994; Woods *et al*., 1998; Xiao *et al*. 1998a, 1998b, 2004; Butterfield, 2000, 2004; see Xiao and Dong, this volume, for a review). Likewise, most taxonomically problematic fossils from the Proterozoic—acritarchs and carbonaceous compressions—are thought to be algal (e.g., Tappan, 1980; Mendelson and Schopf, 1992; Hofmann, 1994; Martin, 1993; Xiao *et al*., 2002). Even *Grypania*, one of the earliest eukaryotic body fossils (<1.9 Ga), is interpreted as an alga (Han and Runnegar, 1992; Schneider *et al*., 2002). The presence of red algae in rocks 1200 Ma necessarily implies that heterotrophs* were present by this time, consistent with molecular clock studies that suggest a diversity of heterotrophic clades in Proterozoic oceans (e.g., Wang *et al*., 1999; Pawlowski *et al*., 2003; Douzery *et al*., 2004; Yoon *et al*., 2004). Yet fossil evidence for Proterozoic heterotrophs is slim. Where are they? Here I review their early fossil record and discuss reasons why fossils of early heterotrophs may be rare.

2. EUKARYOTIC TREE

After much flux, we seem to be converging on a stable phylogeny for eukaryotic organisms (Figure 1; Baldauf, 2003; Simpson and Roger, 2002; Keeling, 2004; Nikolaev *et al*. 2004; Simpson and Roger, 2004; although see, e.g., Philip *et al*., 2005). Most eukaryotes fall into one of six major clades: 1) the opisthokonts, containing the animals and fungi and a few unicellular groups; 2) the amoebozoans, containing the lobose amoebae (both naked and testate) and the slime molds; 3) the plants, containing the red and green algae (and the land plants) and a minor group known as the glaucophytes; 4) the chromalveolates, a clade that itself unites two major groups, the alveolates (containing the dinoflagellates, ciliates, and apicomplexans), and the chromists (including the diatoms, the oomycetes,

* Many members of the Bacteria (=Eubacteria) and Archaea (=Archaebacteria) are also heterotrophic, but I restrict my discussion here to eukaryotic heterotrophs. Thus, when I use the term, 'heterotroph', I am referring only to eukaryotic heterotrophs.

the xanthophyte algae, and the brown algae); 5) the rhizarians, a group characterized by the possession of filose pseudopods, that includes the foraminifera, the (polyphyletic) radiolarians, and the cercozoans; and 6) the excavates, a controversial grouping (Simpson and Roger, 2004) that includes the euglenids and several parasitic taxa such as *Giardia*. Recent gene fusion data suggest that these six clades are divided into two groups: the 'unikonts' (opisthokonts and amoebozoans), and the 'bikonts' (plants, chromalveolates, rhizarians, and excavates), with the root of the eukaryotic tree falling between these two groups (Stechmann and Cavalier-Smith, 2002, 2003).

Heterotrophic taxa are highlighted in Figure 1. Although many eukaryotes are capable of mixotrophy – acquiring nutrition via photosynthesis and phagotrophy, I will restrict my discussion below to those taxa most or all of whose members are strictly heterotrophic. Thus, I will focus on the early fossil record of only five eukaryotic clades: the opisthokonts, the amoebozoans, the chromalveolates, the rhizarians, and the excavates. With few exceptions, all plants are photosynthetic.

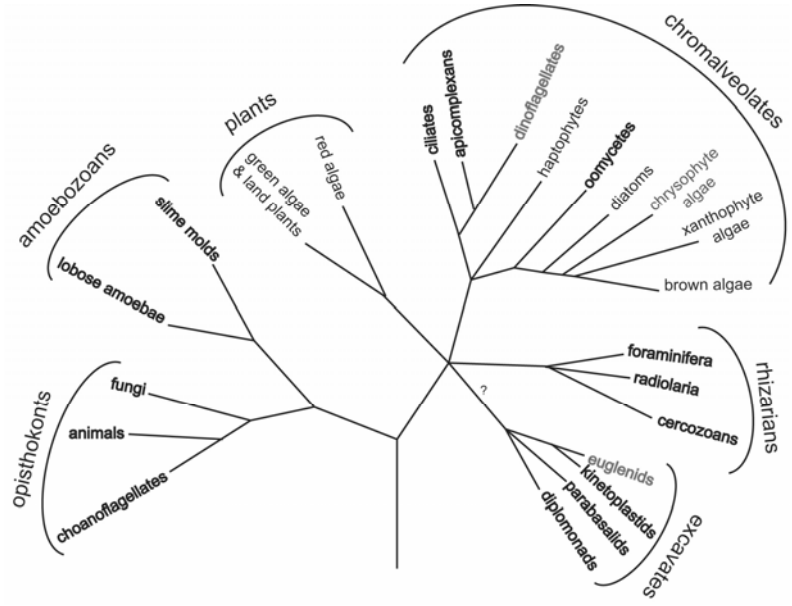


Figure 1. A current view of eukaryote relationships, based on molecular and ultrastructural data (modified from Baldauf 2003; Simpson and Roger, 2002; Keeling, 2004; Nikolaev et al. 2004; Simpson and Roger, 2004). Clades composed primarily of heterotrophs shown in bolded black; clades with both heterotrophs and autotrophs highlighted in gray, and clades composed predominantly of autotrophs shown in plain (non-bold) black. A question mark indicates clades that are not strongly supported (Keeling, 2004). Rooting of the tree is based on gene fusion data (Stechmann and Cavalier-Smith 2002; 2003).

3. FOSSIL EVIDENCE FOR PROTEROZOIC HETEROTROPHS

3.1 Opisthokonts

There are two main opisthokont groups: the animals and the fungi. The Proterozoic fossil record of animals is worthy of an extensive review in its own right; I will not discuss it here except to note that the earliest well accepted evidence for animals are ~580 Ma phosphatized embryos from the Doushantuo Formation, China (Xiao *et al*., 1998b; Xiao and Knoll, 2000; Condon *et al*., 2005). See papers by Jensen *et al*. and Bottjer and Clapham, both in this volume, for further information on Proterozoic animals.

The presence of fungi in the Proterozoic Eon is much more controversial. Several authors have noted similarities between certain microfossils and modern fungi, but in none of these reports has a convincing case been made (e.g., Schopf and Barghoon, 1969; Darby, 1974; Timofeev, 1970; Allison and Awramik, 1989; Schopf, 1968). Some Ediacaran taxa have also been interpreted to be fungal. Retallack (1994), for example, argued that because vendobionts exhibit minimal compaction, they cannot represent soft bodied animals like worms or jellyfish, and instead may be fossilized lichens (an endosymbiotic association between a fungus and an alga). Minimal compaction *has* been observed in some softbodied animals, however (e.g., Hagadorn *et al*., 2002), and, at least in the Ediacaran biota, could be attributed to unusual "death mask" preservation where early diagenetic minerals form a resistant crust (e.g., Gehling 1999). More recently, Peterson *et al*. (2003) argued that Ediacaran fossils from Newfoundland, including *Aspidella*, *Charnia*, and *Charniodiscus*, may represent stem-group fungi. Their argument is based primarily on a process of elimination: the fossils are found in sediments deposited below the photic zone and thus cannot be algal, the fossils do not exhibit evidence for escape or defouling behavior despite having been smothered by a thin layer of ash and thus cannot be animals, and the fossils lack evidence for shrinkage – observed in other Ediacaran taxa – inconsistent, again, with an animal interpretation. As the authors admit, however, there is little positive evidence in the form of fungal-specific characters to support a fungal affinity.

Fungi have also been reported from the 551-635 Ma Doushantuo Formation (Yuan *et al*., 2005). Filaments interpreted to be fungal hyphae occur in lichen-like association with clusters of coccoidal, probably cyanobacterial unicells. A fungal interpretation is based on a combination of characters—dichotomous branching, pyriform terminal structures, absence of sheaths, and narrow diameter (<1μm)—not seen in other filamentous

organisms like cyanobacteria, but comparable to features observed in hyphae of glomalean fungi (Yuan *et al*. 2005).

Even earlier evidence for possible Proterozoic fungi comes from organic-walled microfossils preserved in the 723-1077 Ma Wynniatt Formation, Shaler Supergroup, arctic Canada (Fig. 2A; Butterfield, 2005). These beautifully preserved fossils consist of a large central vesicle with branching, septate, filamentous processes apparently capable of secondary fusion (Figs. 2A-B). Secondary cell-cell fusion is found in both the fungi and the red algae (Gregory, 1984; Graham and Wilcox, 2000), and possibly in the brown algae as well (Butterfield, 2005, and references therein). Because the processes are similar to fungal hyphae, however, Butterfield (2005) specifically compared the Wynniatt fossils with fungi, noting that hyphal fusion is a synapomorphy of the basidiomycetes+ascomycetes (Fig. 2C; Gregory, 1984). Butterfield (2005) referred the Wynniatt fossils to the genus *Tappania*, noting similarities with *Tappania* species from the ~1450 Ma Roper Group, Australia (Javaux *et al*., 2001), and the Meso-Neoproterozoic Ruyang Group, north China (Yin, 1997). Secondary fusion has not been reported in *Tappania*, however, and it is not obvious that the younger and older populations are related.

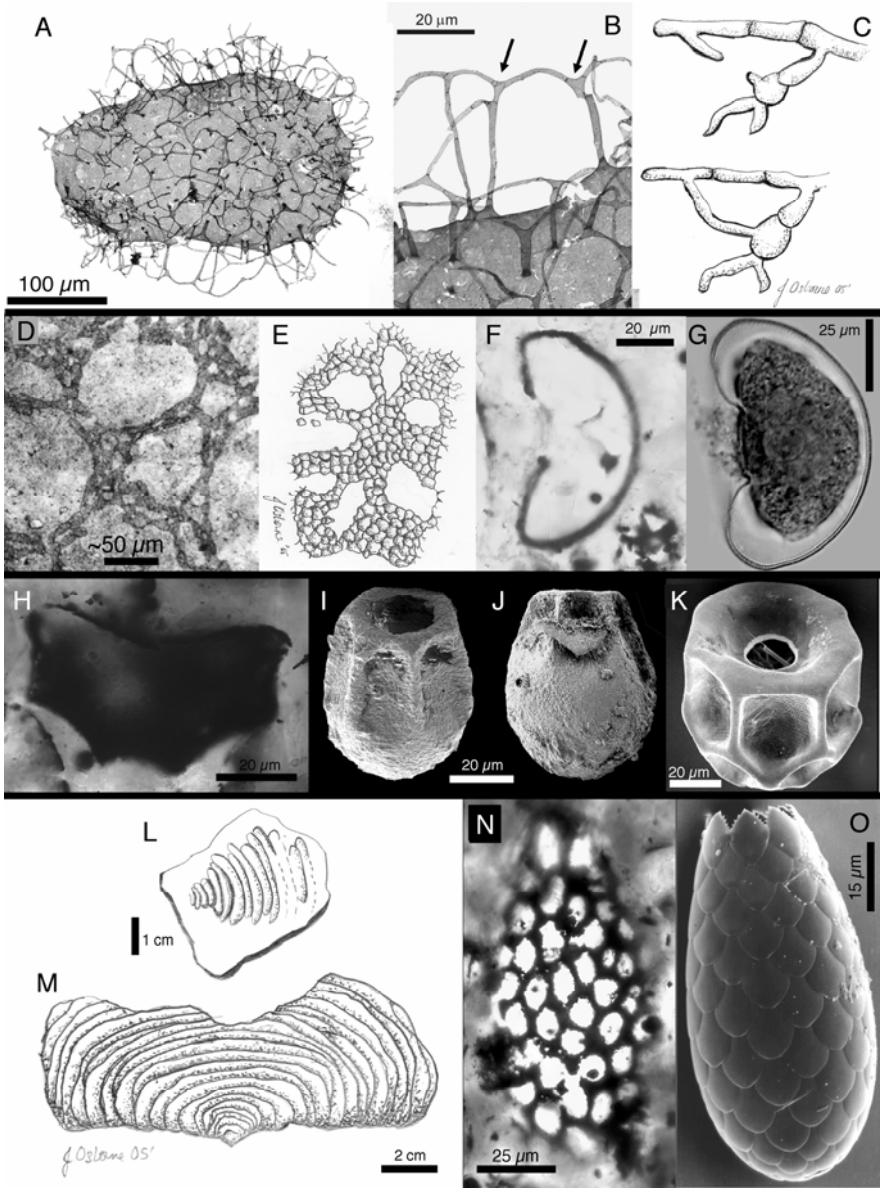
An additional opisthokont group, the unicellular choanoflagellates, produce siliceous 'baskets' ~10-20 μm in size, and thus, could, in principle, have a fossil record (Leadbetter and Thomsen, 2000). No fossil choanoflagellates have been reported, however, from either Proterozoic or Phanerozoic rocks, although this may reflect a lack of search image as much as a lack of preservation.

3.2 Amoebozoans

Amoebozoans comprise two major groups: the slime molds and the lobose amoebae. Slime molds have a very poor fossil record; there are only two occurrences of fossilized slime molds from Phanerozoic rocks, both in Baltic amber (Eocene in age; Dörfelt *et al*., 2003, and references therein). *Eosaccharomyces ramosus*, an unusual organic-walled fossil from ~1000 Ma shales of the Lakhanda Formation, Siberia, consists of open, web-like colonies of cells, a structure reminiscent of the aggregating cells of cellular slime molds (Figs. 2D-E; German, 1979; 1990; Bonner, 1967; Stephenson and Stempen, 1994; Knoll, 1996). The amoeboid cells of modern cellular slime molds lack cell walls, however, and thus have a vanishingly small chance of being preserved in shale. Although displaying a similar behavior, *Eosaccharomyces ramosus* itself is not likely to be a slime mold.

Proterozoic fossil evidence for lobose amoebae comes from vase-shaped microfossils (VSMs), a diverse and globally distributed group of middle

Neoproterozoic (~750 Ma) microfossils that also includes species of possible euglyphid amoebae (see below; Porter and Knoll, 2000; Porter *et al*., 2003). Specifically, three species of VSMs, *Palaeoarcella athanata*, *Melanocyrillium hexodiadema*, and *Hemisphaeriella ornata* (Figs. 2F, 2H-I), possess various combinations of test characters, including an invaginated aperture, regular indentations, and a hemispherical shape, found today only in the Arcellinida, a diverse group of lobose testate amoebae (Figs. 2G, 2J;



Meisterfeld, 2000a; Porter and Knoll, 2000; Porter *et al*., 2003). No exact modern analogs can be identified for *M. hexodiadema* and *H. ornata*, but *P. athanata* is indistinguishable from the modern lobose testate amoeban genus, *Arcella*, suggesting this test morphology may have persisted unchanged from Neoproterozoic times until today. Confirmation of a lobose testate amoeban affinity will depend on a better understanding of test evolution in the Arcellinida, a task currently hindered by poor phylogenetic resolution.

3.3 Chromalveolates

Although accumulating evidence suggests that ancestral chromalveolates were photosynthetic (Keeling, 2004), the clade includes several groups that today are either entirely heterotrophic (e.g., apicomplexans, ciliates, and oomycetes), or are a mix of heterotrophic and photosynthetic taxa (e.g., dinoflagellates). It is not clear when these groups lost their ability to photosynthesize (Keeling, 2004), and thus it is possible that early fossil representatives may have been algal. Nevertheless, I will consider their Proterozoic fossil record here.

Apicomplexans, a group composed entirely of intracellular parasites, do not have a fossil record. Fossil ciliates, on the other hand, can be common, particularly in Upper Jurassic and Lower Cretaceous rocks, where their calcareous tests can be useful in biostratigraphy (Tappan, 1993). Ciliate body fossils are not known from Proterozoic rocks, but evidence for the biomarker gammacerane in the ~742-770 Ma Chuar Group, Grand Canyon, suggests they may have been present by this time (Summons *et al*., 1988; Summons and Walter, 1990). The precursor to gammacerane, tetrahymenol,

Figure 2. (on Page 6) Fossils of putative Proterozoic heterotrophic eukaryotes and their modern analogs. (A-B) A probable fungus. Arrows in (B) indicate points of secondary fusion. Wynniatt Formation, Victoria Island, northwestern Canada. Courtesy of N. J. Butterfield. (C) Hyphal fusion in the fungus, *Botrytis elliptica*, modified from Gregory (1984); no scale bar provided, but individual cells are on the order 5 µm in width. (D) *Eosaccharomyces ramosus*, a possible slime mold. Lakhanda Formation, Siberia. Courtesy of A.H. Knoll. (E) Beginning of cell aggregation in a cellular slime mold, modified from Stephenson and Stempen (1994); no scale bar provided, but individual cells are on the order of 10 µm in size (Bonner, 1967). (F, H-J, N) Vase-shaped microfossils from the Chuar Group, Grand Canyon. (F) *Palaeoarcella athanata*, a probable lobose amoeba. (G) *Arcella hemisphaerica*, a modern lobose amoeba. Courtesy of R. Meisterfeld. (H) *Hemisphaeriella ornata*, a probable lobose amoeba. (I-J) *Melanocyrillium hexodiadema*, a probable lobose amoeba. (K) *Arcella conica*, a modern lobose amoeba. Image courtesy of R. Meisterfeld. (L) *Palaeopascichnus*, a possible foraminiferan from Ediacaran rocks. Modified from Seilacher et al. (2003). (M) The modern xenophyophorean foraminiferan, *Stannophyllum*. Modified from Seilacher et al. (2003). (N) The vase-shaped microfossil, *Melicerion poikilon*, a probable filose amoeba. (O) *Euglypha tuberculata*, a modern filose amoeba. Courtesy of R. Meisterfeld.

is not ciliate-specific, however; it is also known to occur in photosynthetic sulfur bacteria (Kleeman *et al*., 1990), and has even been reported from a fern (Zander *et al*., 1969; Kamaya *et al*., 1991). Gammacerane has also been found in the 1.7 Ga Tuanshanzi Formation of China (Peng *et al*., 1998) but given that there is no fossil evidence for other crown group eukaryotes at this time (Porter, 2004), and, in fact, no undisputed evidence for *any* eukaryotes at this time, it is more conservative to assume that these older biomarkers came from bacteria.

The only claim for Proterozoic oomycetes (Sherwood-Pike, 1991) is based on a single, poorly preserved specimen that was compared by Schopf and Barghoorn (1969) with fungal sporangia. It is possible, however, that other Proterozoic fossils currently interpreted as algae, are actually the remains of oomycetes. Several of the characters found in ~1000 Ma specimens of the fossil *Paleovaucheria*, for example (German, 1981; Woods *et al*., 1998) are also found in oomycetes: sparsely branching tubes with few septa concentrated near the rounded termini, and circular openings at the tips of the termini (Ingold and Hudson, 1993).

Approximately 50% of extant dinoflagellates are heterotrophic (Dodge and Lee, 2000), and although some of these reflect multiple independent losses of plastids, phylogenetic analyses indicate that dinoflagellates may have been ancestrally heterotrophic (Hackett *et al*., 2004, and references therein). The earliest undisputed body fossil evidence for dinoflagellates comes from early Triassic rocks (Fensome *et al*., 1999), but biomarker evidence suggests the group originated at least by early Cambrian time (Moldowan and Talyzina, 1998; Talyzina *et al*., 2000). Dinoflagellate biomarkers have also been reported from several Proterozoic – and even Archean – units, including the 2.78-2.45 Ga Mount Bruce Supergroup, Pilbara Craton, Australia; the ~1400 Ma McMinn Formation, Roper Group, Australia; the ~1100 Ma Nonesuch Formation, Michigan; the ~800 Ma Bitter Springs Formation, Australia; the ~742-770 Ma Chuar Group, Grand Canyon; and the Ediacaran Pertatataka Formation, Australia (Summons and Walter, 1990; Pratt *et al*., 1991; Moldowan *et al*., 2001; Brocks *et al*., 2003a; see also Moldowan *et al*. 1996). Given its age, the Archean occurrence is attributed to an independent (non-dinoflagellate) origin (Brocks *et al*., 2003b), and the Proterozoic occurrences have either been interpreted as possible contaminants (Summons and Walter, 1990; Summons *et al*., 1992) or as dinosteroid precursors that do not by themselves indicate dinoflagellates were present (Moldowan *et al*., 2001).

Interestingly, the pre-Triassic record of dinosteroid abundance correlates well with that of acritarch diversity, suggesting that many acritarchs may represent dinoflagellate cysts (Moldowan *et al*., 1996). Indeed, many modern dinoflagellate cysts lack diagnostic characters, and

would probably be grouped with the acritarchs if found as fossils (Moldowan *et al*., 1996, and references therein). Several papers have suggested certain Proterozoic acritarchs might be dinoflagellate cysts (e.g., Tappan, 1980; Butterfield and Rainbird, 1998, although see Butterfield, 2005; Arouri *et al*., 2000). the most compelling of these is Arouri *et al*. (2000), which showed that some Ediacaran acanthomorphic acritarchs have chemical and ultrastructural characters consistent with a dinoflagellate affinity (although see Versteegh and Blokker, 2004). Because the taxonomic distribution of these characters is not well documented, however, it is impossible to know whether their occurrence in both fossil and modern groups is due to homology or convergence, and, if due to homology, whether their occurrence reflects a shared derived feature of the dinoflagellates or a plesiomorphic condition.

3.4 Rhizarians

Rhizarians include three major groups, foraminifera, cercozoans, and radiolarians. The last of these is polyphyletic; recent phylogenies suggest that phaeodareans, traditionally grouped with the other radiolarian classes, polycystineans and acanthareans, are derived from within cercozoans (Nikolaev *et al*., 2004). With a few exceptions (e.g., *Paulinella,* chlorarachniophytes), all rhizarians are obligate heterotrophs.

Radiolarians are not known from Precambrian rocks. The earliest fossil evidence for radiolarians is polycystinean skeletons from the Middle Cambrian (Won *et al*., 1999). Acantharians lack a fossil record—their strontium sulfate skeletons dissolve easily in seawater—and the oldest phaeodareans are Cretaceous (Danelian and Moreira, 2004, and references cited therein).

The earliest undisputed foraminifera are from Early Cambrian rocks (Culver, 1991, 1994; McIlroy *et al*., 2001), although Seilacher *et al*. (2003) have made an interesting case that some Ediacaran taxa were giant foraminifera (also see Zhuravlev, 1993). Specifically, Seilacher and his colleagues argue that several Ediacaran trace fossils, including *Palaeopascichnus*, *Neonereites*, *Intrites*, and *Yelovichnus*, are xenophyophoreans[*], giant foraminifera up to 25 cm in size that today are known only from abyssal environments (Figs. 2L, 2N; Gooday and Tendal, 2000; Pawlowski *et al*., 2003). They also interpret vendobionts as extinct

[*] To be exact, Seilacher *et al*. (2003) interpret vendobionts as an extinct group of giant rhizopods. As originally construed, however, rhizopods are polyphyletic. The group was recently revised and renamed 'Cercozoa' (Cavalier-Smith, 1998). Presumably Seilacher *et al*. are interpreting the vendobionts as close relatives of xenophyophoreans.

foraminifera, arguing that the sand-filled, fecal 'skeletons' ('stercomare') found inside the tests of xenophyophoreans may be a modern analog for the sand-filled bodies of some vendobionts (Grazhdankin and Seilacher, 2002).

A recent study suggests that cercozoans may be among the most diverse protozoan groups alive today, comparable in diversity to the ciliates (Bass and Cavalier-Smith, 2004). The majority of cercozoans are zooflagellates, taxa that would be unlikely to fossilize, but the group also includes filose amoebae, some of which possess fossilizable tests. Possible evidence for Proterozoic cercozoans is the 742-770 Ma vase-shaped microfossil, *Melicerion poikilon* (Fig. 2N), thought to be the remains of a filose testate amoeba (Porter and Knoll, 2000; Porter *et al*., 2003). Specifically, *Melicerion* possessed a tear-drop-shaped, aperturate test with circular, regularly arranged, mineralized scales embedded in an organic wall (Porter *et al*., 2003). This character combination is known today only in the euglyphid amoebae, a monophyletic group of filose testate amoebae (Fig. 2O; Meisterfeld, 2000b; Wylezich *et al*., 2002). Some lobose testate amoebae also make tests with mineralized scales, but the scales are different in shape or less regularly arranged (Meisterfeld, 2000b). Interestingly, there is a group of lobose testate amoebae that *do* have circular scales in their tests, but these are not endogenous; i.e. they are acquired by engulfing euglyphid tests and stealing the scales (Gnekow, 1981). Given that there is good evidence for lobose testate amoebae in rocks of this age (see Section 3.2), *Melicerion* could be interpreted as a lobose amoeba, but its strong similarities with euglyphids support a closer tie with cercozoans.

3.5 Excavates

There are no reports of excavate taxa from Proterozoic rocks. Most excavates have extremely low preservation potential, but putative evidence for fossil euglenids in fluvial and nearshore-marine rocks from Ordovician and Silurian strata (Gray and Boucot, 1989) suggests the organic pellicle found in euglenids may be preservable. This is consistent with studies of Lindgren (1981) showing that the lorica of the euglenid *Trachelomonas* is acid-resistant. Possible euglenids are also known, along with kinetoplastids, from amber (Schönborn *et al*., 1999; Poinar and Poinar, 2004), although this preservational window does not extend into the Proterozoic Eon.

3.6 Summary

Table 1 summarizes the fossil evidence for heterotrophic eukaryotes in Proterozoic rocks. There are several reports of heterotrophic taxa from the Proterozoic, but only four of these – animals, fungi, lobose amoebae, and,

Table 1. Fossil evidence for possible heterotrophic protists in Proterozoic (and Archean) rocks. See text for more details.

Taxon	Proterozoic Fossil Evidence	Age (Ma)	Reference
Opisthokonts			
Fungi	*Aspidella*, *Charniodiscus*, *Charnia,* etc.	575-542	Peterson *et al*., 2003
" "	Fungal hyphae in a lichen-like association	635-551	Yuan *et al.*, 2005
" "	Acritarchs exhibiting secondary cell fusion	>723-1077	Butterfield, 2005
Amoebozoans			
Lobose amoebae	*Palaeoarcella athanata, Melanocyrillium hexodiadema, Hemisphaeriella ornata*	742-770	Porter *et al*., 2003
Chromalveolates			
Ciliates	gammacerane (biomarker)	742-770	Summons *et al*., 1988; Summons and Walter, 1990
" "	" "	~1700	Peng *et al*., 1998
Dinoflagellates	dinosterane (biomarker)	~540-630	Summons and Walter, 1990
" "	" "	~742-770	Moldowan *et al*., 2001
" "	" "	~800	Summons and Walter, 1990
" "	" "	~1100	Pratt *et al*., 1991
" "	" "	~1400	Moldowan *et al*. 2001
" "	" "	~2780 - 2450	Brocks *et al*., 2003a,b
Rhizarians			
Foraminifera	vendobionts, *Palaeopascichnus, Neonereites, Intrites, Yelovichnus,* etc.	575-542	Zhuravlev, 1993; Seilacher *et al*., 2003
Cercozoans	*Melicerion poilon*	742-770	Porter and Knoll, 2000; Porter *et al*., 2003

probably, filose amoebae -- are based on specific characters that are likely to be synapomorphies for the group in question (or for clades within the group). The other reports listed in Table 1 are plausible but either lack specific synapomorphies linking fossils to their modern counterparts or – in the case of biomarker evidence – may be contaminants.

Granted the risks in making generalizations about the sparse Proterozoic fossil record, we can still make a few interesting observations. The first,

already noted above, is that although today the diversity of heterotrophs exceeds that of algae, during the Proterozoic the situation seems reversed. The second is that although heterotrophs are ancestral to the algae, the first convincing algal fossils precede the first convincing heterotroph fossils by several hundred million years. Why are heterotrophs rare in Proterozoic rocks?

4. WHY ARE HETEROTROPHS RARE IN PROTEROZOIC ROCKS?

Porter and Knoll (2000) offered two reasons why few, if any, heterotrophs are found in rocks older than ~770-800 Ma (when VSMs first appear). The first is that heterotroph diversity may have been low due to limited primary productivity in Mesoproterozoic oceans. Evidence for limited productivity during this interval comes primarily from theoretical arguments. Anbar and Knoll (2002), for example, have argued that if Mesoproterozoic oceans were anoxic and sulfidic below the mixed layer (Canfield, 1998; Shen *et al*., 2002, 2003; Arnold *et al*., 2004; Brocks *et al*., 2005), then both dissolved iron and molybdenum would have been scarce. As both elements are important components of enzymes responsible for nitrogen fixation and nitrate assimilation, they reason that nitrogen cycling would have been limited in Mesoproterozoic oceans. Further support for a nitrogen-stressed biosphere during this time comes from box models that show that as oxygen levels rose during the early Proterozoic, increasing levels of nitrification and denitrification would have lowered the pool of bioavailable nitrogen (Fennel *et al*., 2005).

Empirical evidence for limited primary productivity is more problematic. Anbar and Knoll (2002) point out that the average value of $\partial^{13}C$ in Mesoproterozoic carbonates is ~1.5‰ lower than in Paleoproterozoic, Neoproterozoic, and Phanerozoic carbonates, suggesting depressed Mesoproterozoic primary productivity. Nonetheless, late Paleoproterozoic and early Mesoproterozoic $\partial^{13}C$ values hover around 0‰, indicating that organic carbon burial constituted a significant proporation—~20%—of total carbon burial; average values near 3.5‰ from late Mesoproterozoic rocks (Frank *et al*., 2003) suggest even higher proportions. Of course, because organic carbon burial rates are a function of several factors, including sedimentation rates and redox conditions, they may not be reliable indicators of primary productivity levels at all, high or low. Anbar and Knoll also point out that several Mesoproterozoic basins appear to have had limited depth gradients in the isotopic composition of DIC, consistent with low productivity. Limited gradients could also reflect vigorous ocean mixing,

however, or a large DIC reservoir (Bartley and Kah, 2004) that effectively drowned out any signal of $\delta^{13}C$ stratification resulting from high productivity.

Anbar and Knoll (2002) emphasize that the primary organisms affected by nitrogen stress would be eukaryotic algae, which, unlike cyanobacteria, are unable to fix nitrogen or to scavenge bioavailable nitrogen from their surroundings. Thus, even if overall primary productivity was not limited, it is expected that eukaryotic primary productivity was. How would eukaryotic heterotrophs have been impacted? Because they can get bioavailable nitrogen by ingesting organic particles, they are not directly affected by a nitrogen-stressed world. They may have been indirectly affected, however, simply because limited overall primary productivity means limited food supply. But if only eukaryotic algae were negatively impacted, it's not clear that eukaryotic heterotrophs themselves would have been; they could have dined primarily on bacteria, as many do today. Assuming the nutritive content of bacteria and eukaryotic algae is similar, then heterotrophic eukaryotes would have been abundant and diverse in Mesoproterozoic oceans.

More likely, the dearth of heterotrophs prior to ~770 Ma reflects taphonomic bias (Porter and Knoll, 2000). Although both algae and heterotrophs make mineralized structures, with few exceptions (Allison and Hilgert, 1986; Grant, 1990; Horodyski and Mankiewicz, 1990; Watters and Grotzinger, 2001; Wood *et al*., 2002; Porter *et al*., 2003), there are no mineralizing eukaryotes – algal or heterotrophic – from the Precambrian. The Precambrian body fossil record thus primarily comprises organic-walled structures, and within these taphonomic limits, algae have an important advantage. Unlike the majority of heterotrophs, which require a flexible membrane for phagocytosis, most algae possess cell walls. Indeed, cell walls have evolved multiple times, suggesting that, as long as the organism doesn't depend on phagocytosis, having rigid support is advantageous (cf., Leander, 2004). The presence of a cell wall by itself may not impart significant preservational advantages (e.g., Bartley, 1996; de Leeuw and Largeau, 1993), but several algal groups impregnate their walls with highly resistant macromolecules. These include algaenans, which occur in the cell walls or cysts of some green algae, some eustigmatophytes (a group of chromist algae), and the photosynthetic dinoflagellate *Gymnodinium catenatum* (Gelin *et al*., 1997, 1999; Versteegh and Blokker, 2004); and dinosporin, which occurs in the resting cysts of dinoflagellates (Versteegh and Blokker, 2004). These groups in particular should be well represented among Proterozoic organic-walled fossil protists.

Heterotrophs do make preservable organic-walled structures, however. The fossilized tests of amoebae have been found in a variety of facies,

indicating their preservation does not depend on exceptional taphonomic circumstances (Medioli *et al*. 1990; Porter and Knoll, 2000). Loricae of folliculinid ciliates reported from cherts in Africa indicate these organic-walled structures may also be preserved (Deflandre and Deunff, 1957). Many heterotrophs also make organic-walled cysts, including several naked (non-testate) amoebae (Lee *et al*., 2000). The degradation-resistance of these structures is not well known, although probable cysts preserved in some fossil testate amoebae suggest it may be relatively good (Martí-Mus and Moczydlowska, 2000; Porter *et al*., 2003). In addition, fungi, oomycetes, and heterotrophic dinoflagellates have cell walls; either they are osmotrophs, able to transport dissolved organic matter across this rigid boundary, or, in the case of dinoflagellates, they phagocytose by opening their thecal plates and extruding a pseudopod-like structure (Hackett *et al*., 2004). Their walls are about as resistant as algal cell walls, if not more so (de Leeuw and Largeau, 1993). Finally, highly resistant macromolecules similar to algaenans and dinosporins are known from fungal spores (de Leeuw and Largeau, 1993).

Algae have a taphonomic advantage then, *not* because heterotrophs are inherently *un*preservable, but because more algae make preservable structures than heterotrophs do. Most algae have cell walls, for example, while most heterotrophs do not. If the majority of Precambrian acritarchs are the remains of vegetative cells rather than cysts (Butterfield, 2004), then, statistically speaking, most acritarchs probably are algal. But there is no good reason to think *all* of them are algal (Butterfield, 2005). Cell walls, cysts, and spores of heterotrophs may constitute a sizable – though unrecognized -- minority of the Precambrian fossil record.

5. CONCLUSIONS

Although heterotrophic eukaryotes necessarily preceded eukaryotic algae, the latter are much better represented in the Proterozoic fossil record. Convincing evidence exists for only four heterotrophic clades during this time: the fungi, known from ~580 Ma rocks, and possibly from rocks older than 723 Ma; the lobose and filose amoebae, which appear in rocks 742-770 Ma; and the animals, which appear near the close of the Proterozoic Eon. Other Proterozoic body fossils or biomarkers may represent ciliates, dinoflagellates, oomycetes, and foraminifera. The dearth of Proterozoic fossil heterotrophs may reflect low heterotroph diversity caused by limited primary productivity. More likely, however, it reflects a preservational bias among organic-walled fossils: more algae make preservable organic-walled structures than heterotrophs do. Nonetheless, heterotrophs do make

preservable structures, and their cysts, spores, and tests probably go unrecognized among the problematic fossils that constitute the bulk of the Precambrian fossil record.

ACKNOWLEDGMENTS

I am thankful to Shuhai Xiao and Jay Kaufman for inviting me to contribute to this volume, and to Stan Awramik, David Chapman, Linda Kah, Andrew Knoll, David Lamb, Brian Leander, and Alastair Simpson for useful discussions and feedback. Jennifer Osborne provided illustrations, and Shuhai Xiao, Carl Mendelson, and Nick Butterfield provided useful and constructive reviews.

REFERENCES

Allison, C. W., and Awramik, S. M., 1989, Organic-walled microfossils from the earliest Cambrian or latest Proterozoic Tindir Group rocks, northwest Canada, *Precambrian Res.* **43**: 253-294.

Allison, C. W., and Hilgert, J. W., 1986, Scale microfossils from the Early Cambrian of Northwest Canada, *J. Paleont.* **60**(5): 973-1015.

Anbar, A. D., and Knoll, A. H., 2002, Proterozoic ocean chemistry and evolution: a bioinorganic bridge? *Science* **297**: 1137-1142.

Andersson, J. O., and Roger, A. J., 2002, A cyanobacterial gene in nonphotosynthetic protists—an early chloroplast acquisition in eukaryotes? *Curr. Biol.* **12**: 115-119.

Arnold, G. L., Anbar, A. D., Barling, J., and Lyons, T. W., 2004, Molybdenum isotope evidence for widespread anoxia in mid-Proterozoic oceans, *Science*, **304**: 87-90.

Arouri, K. R., Greenwood, P. F., and Walter, M. R., 2000, Biological affinities of Neoproterozoic acritarchs from Australia: microscopic and chemical characterisation, *Org. Geochem.* **31**: 75-89.

Baldauf, S. L., 2003, The deep roots of eukaryotes, *Science* **300**: 1703-1706.

Bartley, J. K., 1996, Actualistic taphonomy of Cyanobacteria: implications for the Precambrian fossil record, *Palaios* **11**: 571-586.

Bartley, J. K., and Kah, L. C., 2004, Marine carbon reservoir, C-org-C-carb coupling, and the evolution of the Proterozoic carbon cycle, *Geology* **32**: 129-132.

Bass, D., and Cavalier-Smith, T., 2004, Phylum-specific environmental DNA analysis reveals remarkably high global biodiversity of Cercozoa (Protozoa), *Int. J. Syst. Evol. Microbiol.* **54**: 2393-2404.

Bonner, J. T., 1967, *Cellular Slime Molds*, Princeton University Press, Princeton, New Jersey.

Brocks, J. J., Buick, R., Logan, G. A., and Summons, R. E., 2003a, Composition and syngeneity of molecular fossils from the 2.78 to 2.45 billion-year-old Mount Bruce Supergroup, Pilbara Craton, Western Australia, *Geochim. Cosmochim. Acta* **67**: 4289-4319.

Brocks, J. J., Buick, R., Summons, R. E., and Logan, G. A., 2003b, A reconstruction of Archean biological diversity based on molecular fossils from the 2.78 to 2.45 billion-year-old Mount Bruce Supergroup, Hamersley Basin, Western Australia, *Geochim. Cosmochim. Acta* **67**: 4321-4335.

Brocks, J. J., Love, G. D., Summons, R. E., Knoll, A.H., Logan, G. A, Bowden, S. A., 2005, Biomarker evidence for green and purple sulfur bacteria in a stratified Palaeoproterozoic sea, *Nature* **437**: 866-870.

Butterfield, N. J., 2000, *Bangiomorpha pubescens* n. gen., n. sp.: implications for the evolution of sex, multicellularity, and the Mesoproterozoic-Neoproterozoic radiation of eukaryotes, *Paleobiology* **26**: 386-404.

Butterfield, N. J., 2004, A vaucheriacean alga from the middle Neoproterozoic of Spitsbergen: implications for the evolution of Proterozoic eukaryotes and the Cambrian explosion, *Paleobiology* **30**: 231-252.

Butterfield, N. J., 2005, Probable Proterozoic Fungi, *Paleobiology* **31**: 165-182.

Butterfield, N. J., and Rainbird, R. H., 1998, Diverse organic-walled fossils, including "possible dinoflagellates" from the early Neoproterozoic of arctic Canada, *Geology* **26**: 963-966.

Butterfield, N. J., Knoll, A. H., and Swett, K., 1990, A bangiophyte red alga from the Proterozoic of arctic Canada, *Science* **250**: 104-107.

Butterfield, N. J., Knoll, A. H., and Swett, K., 1994, Paleobiology of the Neoproterozoic Svanbergfjellet Formation, Spitsbergen, *Fossils Strata* **34**: 1-84.

Canfield, D. E., 1998, A new model for Proterozoic ocean chemistry, *Nature* **396**: 450-453.

Cavalier-Smith, T., 1998, A revised six-kingdom system of life, *Biol. Rev.* **73**: 203-266.

Condon, D., Zhu, M., Bowring, S., Wang, W., Yang, A., and Jin, Y., 2005, U-Pb ages from the Neoproterozoic Doushantuo Formation, China, *Science* **308**: 95-98.

Culver, S. J., 1991, Early Cambrian Foraminifera from West Africa, *Science* **254**: 689-691.

Culver, S. J., 1994, Early Cambrian Foraminifera from the southwestern Taoudeni Basin, West Africa, *J. Foram. Res.* **24**: 191-202.

Danelian, T., and Moreira, D., 2004, Palaeontological and molecular arguments for the origin of silica-secreting marine organisms, *C. R. Palevol* **3**: 229-236.

Darby, D. G., 1974, Reproductive modes of *Huroniospora microreticulata* from cherts of the Precambrian Gunflint Iron-Formation, *Geol. Soc. Amer. Bull.* **85**: 1595-1596.

de Leeuw, J. W., and Largeau, C., 1993, A review of macromolecular organic compounds that comprise living organisms and their role in kerogen, coal, and petroleum formation, in: *Organic Geochemistry: Principles and Applications* (M. H. Engel and S. A. Macko, eds.), Topics in Geobiology, Plenum Press, New York, pp. 23-72.

Deflandre, G., and Deunff, J., 1957, Sur la presence de cilies fossiles de la familie des Folliculinidae dans un silex du Gabon, *C. R. Hebd. Séances Acad. Sci.* **244**: 3090-3093.

Dodge, J. D., and Lee, J. J., 2000, Phylum Dinoflagellata Bütschli, 1885, in: *An Illustrated Guide to the Protozoa* (J. J. Lee, G. F. Leedale and P. Bradbury, eds.), Society of Protozoologists, Lawrence, Kansas, pp. 656-689.

Dörfelt, H., Schmidt, A. R., Ullman, P., and Wunderlick, J., 2003, The oldest myxogastrid slime mold, *Mycol. Res.* **107**: 123-126.

Douzery, E. J. P., Snell, E. A., Bapteste, E., Delsuc, F., and Philippe, H., 2004, The timing of eukaryotic evolution: does a relaxed molecular clock reconcile proteins and fossils?, *Proc.*

Natl. Acad. Sci. USA **101**: 15386-15391.

Fennel, K., Follows, M., and Falkowski, P.G., 2005, The co-evolution of the nitrogen, carbon,and oxygen cycles in the Proterozoic ocean, *Am. J. Sci.* **305**: 526-545.

Fensome, R. A., Saldarriaga, J. F., and Taylor, F. J. R., 1999, Dinoflagellate phylogeny revisited: reconciling morphological and molecular based phylogenies, *Grana* **38**: 66-80.

Frank, T. D., Kah, L. C., and Lyons, T. W., 2003, Changes in organic matter production and accumulation as a mechanism for isotopic evolution in the Mesoproterozoic ocean, *Geol. Mag.* **140**: 397-420.

Gehling, J. G., 1999, Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks, *Palaios* **14**: 40-57.

Gelin, F., Boogers, I., Noordeloos, A. A. M., Damsté, J. S. S., Riegman, R., and Leeuw, J. W. d., 1997, Resistant biomacromolecules in marine microalgae of the classes Eustigmatophyceae and Chlorophyceae: geochemical implications, *Org. Geochem.* **26**: 659-675.

Gelin, F., Volkman, J. K., Largeau, C., Derenne, S., Damsté, J. S. S., and Leeuw, J. W. D., 1999, Distribution of aliphatic, nonhydrolyzable biopolymers in marine microalgae, *Org. Geochem.* **30**: 147-159.

German, T., 1979, Nakhodki gribov v Rifee (Discoveries of fungi in the Riphean), in: *Paleontologiia Dokembriia i Rannego Kembriia* (B. Sokolov, ed.), Nauka, Leningrad, pp. 129-136.

German, T., 1981, Nitchatye mikroorganizmy Lakhandinskoi svity reki Mai [Filamentous microorganisms in the Lakhanda Formation on the Maya River], *Paleontol. Zh.* **1981**(2): 100-107.

German, T. N., 1990, *Organic World Billion Year Ago*, Nauka, Leningrad.

Gnekow, M. A., 1981, Beobachtungen zur Biologie und Ultrastruktur der moobewohnenden Thecamöbe *Nebela tincta* (Rhizopoda). *Arch. Protistenkd.* **124**: 36-69.

Gooday, A. J., and Tendal, O. S., 2000, Class Xenophyophorea Schulze, 1904, in: *An Illustrated Guide to the Protozoa* (J. J. Lee, G. F. Leedale, and P. Bradbury, eds.), Society of Protozoologists, Lawrence, Kansas, pp. 1086-1097.

Graham, L. E., and Wilcox, L. W., 2000, *Algae*, Prentice Hall, Upper Saddle River, NJ.

Grant, S. W. F., 1990, Shell structure and distribution of *Cloudina*, a potential index fossil for the terminal Proterozoic, *Am. J. Sci.* **290A**: 261-294.

Gray, J., and Boucot, A. J., 1989, Is *Moyeria* a euglenoid?, *Lethaia* **22**: 447-456.

Grazhdankin, D., and Seilacher, A., 2003, Underground Vendobionta from Namibia, *Palaeontology* **45**: 57-78.

Gregory, P. H., 1984, The fungal mycelium: an historical perspective, *Trans. Br. Mycol. Soc.* **82**: 1-11.

Hackett, J. D., Anderson, D. M., Erdner, D. L., and Bhattacharya, D., 2004, Dinoflagellates: a remarkable evolutionary experiment, *Am. J. Bot.* **91**: 1523-1534.

Hagadorn, J. W., Dott, R. H., and Damrow, D., 2002, Stranded on an Upper Cambrian shoreline: Medusae from central Wisconsin, *Geology* **30**: 103-106.

Han, T.-M., and Runnegar, B. 1992, Megascopic eukaryotic algae from the 2.1-billion-year-old Negaunee Iron-Formation, Michigan, *Science* **257**: 232-235.

Hofmann, H. J., 1994, Proterozoic carbonaceous compressions ("metaphytes" and "worms"), in: *Early Life on Earth* (S. Bengtson, ed), Columbia University Press, New York, pp. 342-

357.

Horodyski, R. J., and Mankiewicz, C., 1990, Possible Late Proterozoic skeletal algae from the Pahrump Group, Kingston Range, southeastern California, *Am. J. Sci.* **290A**: 149-169.

Ingold, C. T., and Hudson, H. J., 1993, *The Biology of Fungi*, Chapman and Hall, New York.

Javaux, E. J., Knoll, A. H., and Walter, M. R., 2001, Morphological and ecological complexity in early eukaryotic ecosystems, *Nature* **412**: 66-69.

Kamaya, R., Mori, T., Shoji, H., Ageta, H., Chang, H. C., and Hsu, H. Y., 1991, Fern constituents: triterpenes from *Oleandra wallichii*, *Yakugaku Zasshi (J. Pharmaceutical Soc. Japan)*, **11**: 120-125.

Keeling, P. J., 2004, Diversity and evolutionary history of plastids and their hosts, *Am. J. Bot.* **91**: 1481-1493.

Kleemann, G., Poralla, K., Englert, G., Kjosen, H., Liaaen-jensen, N., Neunlist, S., and Rohmer, M., 1990, Tetrahymanol from the phototrophic bacterium *Rhodopseudomonas palustris*: first report of a gammacerane triterpene from a prokaryote, *J. Gen. Microbiol.* **136**: 2551-2553.

Knoll, A. H., 1996, Archean and Proterozoic paleontology, in: *Palynology: Principles and Applications* (J. Jansonius and D. C. McGregor, eds.), American Association of Stratigraphic Palynologists Foundation, pp. 51-80.

Leadbetter, B. S. C., and Thomsen, H. A., 2000, Order Choanoflagellida, Kent, 1880, *An Illustrated Guide to the Protozoa, Second Edition* (J. J. Lee, G. F. Leedale, and P. Bradbury, eds.), Allen Press, Lawrence, Kansas, pp. 14-38.

Leander, B. S., 2004, Did trypanosomatid parasites have photosynthetic ancestors?, *Trends Microbiol.* **12**: 251-258.

Lee, J. J., Leedale, G. F., and Bradbury, P. (eds.), 2000, *An Illustrated Guide to the Protozoa*, Society of Protozoologists, Lawrence, KS.

Lindgren, S., 1981, Remarks on the taxonomy, botanical affinities, and distribution of leiospheres, *Stockh. Contr. Geol*. **38**: 1-20.

Martí Mus, M., and Moczydlowska, M., 2000, Internal morphology and taphonomic history of the Neoproterozoic vase-shaped microfossils from the Visingsö Group, Sweden, *Norsk Geol. Tidsskr.* **80**: 213-228.

Martin, F., 1993, Acritarchs: a review, *Biol. Rev.* **68**: 475-538.

McIlroy, D., Green, O. R., and Brasier, M. D., 2001, Palaeobiology and evolution of the earliest agglutinated Foraminifera: *Platysolenites*, *Spirosolenites* and related forms, *Lethaia* **34**: 13-29.

Medioli, F. S., Scott, D. B., Collins, E. S., and McCarthy, F. M. G., 1990, Fossil thecamoebians: present status and prospects for the future, in: *Paleoecology, Biostratigraphy, Paleoceanography and Taxonomy of Agglutinated Foraminifera* (C. Hemleben *et al*., eds.), Kluwer Academic, Dordrecht, Netherlands, pp. 813-839.

Meisterfeld, R., 2000a, Order Arcellinida Kent, 1880, in: *An Illustrated Guide to the Protozoa* (J. J. Lee, G. F. Leedale, and P. Bradbury, eds.), Society of Protozoologists, Lawrence, Kansas, pp. 827-860.

Meisterfeld, R., 2000b, Testate amoebae with filopodia, in: *An illustrated guide to the Protozoa* (J. J. Lee, G. F. Leedale, and P. Bradbury, eds,), Society of Protozoologists, Lawrence, Kansas, pp. 1054-1084.

Mendelson, C. V., and Schopf, J. W., 1992, Proterozoic and Early Cambrian acritarchs, in:

The Proterozoic Biosphere (J. W. Schopf and C. Klein, eds.), Cambridge University Press, Cambridge, pp. 219-232.

Moldowan, J. M., and Talyzina, N. M., 1998, Biogeochemical evidence for dinoflagellate ancestors in the Early Cambrian, *Science* **281**: 1168-1170.

Moldowan, J. M., Dahl, J., Jacobsen, S. R., Huizinga, B. J., Fago, F. J., Shetty, R., Watt, D. S., and Peters, K. E., 1996, Chemostratigraphy reconstruction of biofacies: molecular evidence linking cyst-forming dinoflagellates with pre-Triassic ancestors, *Geology* **24**: 159-162.

Moldowan, J. M., Jacobsen, S. R., Dahl, J., Al-Hajji, A., Huizinga, B. J., and Fago, F. J., 2001, Molecular fossils demonstrate Precambrian origins of dinoflagellates, in: *The Ecology of the Cambrian Radiation* (A. Yu. Zhuravlev and R. Riding, eds.), Columbia University Press, New York, pp. 475-493.

Nikolaev, S. I., Berney, C., Fahrni, J. F., Bolivar, I., Polet, S., Mylnikov, A. P., Aleshin, V. V., Petrov, N. B., and Pawlowski, J., 2004, The twilight of Heliozoa and rise of Rhizaria, an emerging supergroup of amoeboid eukaryotes, *Proc. Natl. Acad. Sci. USA* **101**: 8066-8071.

Pawlowski, J., Holzmann, M., Fahrni, J., and Richardson, S. L., 2003, Small subunit ribosomal DNA suggests that the xenophyophorean *Syringammina corbicula* is a foraminiferan, *J. Eukaryot. Microbiol.* **50**: 483-487.

Peng, P., Sheng, G., Fu, J., and Yan, Y., 1998, Biological markers in 1.7 billion year old rock from the Tuanshanzi Formation, Jixian strata section, North China, *Org. Geochem.* **29**: 1321-1329.

Peterson, K. J., Waggoner, B., and Hagadorn, J. W., 2003, A fungal analog for Newfoundland Ediacaran fossils, *Integr. Comp. Biol.* **43**: 127-136.

Philip, G. A., Creevey, C. J., and McInerney, J. O., 2005, The Opisthokonta and the Ecdysozoa may not be clades: stronger support for the grouping of plant and animal than for animal and fungi and stronger support for the Coelomata than Ecdysozoa, *Molec. Biol. Evol.* **22**: 1175-1184.

Poinar, G., and Poinar, R., 2004, *Paleoleishmania proterus* n. gen., n. sp., (Trypanosomatidae: Kinetoplastida) from Cretaceous Burmese amber, *Protist* **155**: 305-310.

Porter, S. M., 2004, The fossil record of early eukaryotic diversification, *Paleontol. Soc. Papers* **10**: 35-50.

Porter, S. M., and Knoll, A. H., 2000, Testate amoebae in the Neoproterozoic Era: evidence from vase-shaped microfossils in the Chuar Group, Grand Canyon, *Paleobiology* **26**: 360-385.

Porter, S. M., Meisterfeld, R., and Knoll, A. H., 2003, Vase-shaped microfossils from the Neoproterozoic Chuar Group, Grand Canyon: a classification guided by modern testate amoebae, *J. Paleontol.* **77**: 409-429.

Pratt, L. M., Summons, R. E., and Hieshima, G. B., 1991, Sterane and triterpane biomarkers in the Precambrian Nonesuch Formation, North American Midcontinent Rift, *Geochim. Cosmochim. Acta* **55**: 911-916.

Retallack, G. J., 1994, Were the Ediacaran fossils lichens? *Paleobiology* **20**: 523-544.

Schneider, D. A., Bickford, M. E., Cannon, W. F., Sculz, K. J., and Hamilton, M. A., 2002, Age of volcanic rocks and syndepositional iron formations, Marquette Range Supergroup:

implications for the tectonic setting of Paleoproterozoic iron formations of the Lake Superior region, *Can. J. Earth Sci.* **39**: 999-1012.

Schönborn, W., Dörfelt, H., Foissner, W., Krienitz, L., and Schäfer, U., 1999, A fossilized microcenosis in Triassic amber, *J. Eukaryot. Microbiol.* **46**: 571-584.

Schopf, J. W., 1968, Microflora of the Bitter Springs Formation, Late Precambrian, central Australia, *J. Paleontol.* **42**: 651-688.

Schopf, J. W., and Barghoorn, E. S., 1969, Microorganisms from the late Precambrian of South Australia, *J. Paleontol.* **43**: 111-118.

Seilacher, A., Grazhdankin, D., and Legouta, A., 2003, Ediacaran biota: the dawn of animal life in the shadow of giant protists, *Paleontol. Res.* **7**: 43-54.

Shen, Y, Canfield, D.E., and Knoll, A.H., 2002, Middle Proterozoic ocean chemistry: evidence from the McArthur Basin, northern Australia, *Am. J. Sci.* **302**: 81-109.

Shen, Y., Knoll, A.H., and Walter, M. R., 2003, Evidence for low sulphate and anoxia in a mid-Proterozoic marine basin, *Nature* **423**: 632-635.

Sherwood-Pike, M., 1991, Fossils as keys to evolution in fungi, *BioSystems* **25**: 121-129.

Simpson, A. G. B., and Roger, A. J., 2002, Eukaryotic evolution: getting to the root of the problem, *Curr. Biol.* **12**: R691-R693.

Simpson, A. G. B., and Roger, A. J., 2004, The real 'kingdoms' of eukaryotes, *Curr. Biol.* **14**: R693-R696.

Stechmann, A., and Cavalier-Smith, T., 2002, Rooting the eukaryote tree by using a derived gene fusion, *Science* **297**: 89-91.

Stechmann, A., and Cavalier-Smith, T., 2003, The root of the eukaryote tree pinpointed, *Curr. Biol.* **13**: R665-R666.

Stephenson, S. L., and Stempen, H., 1994, *Myxomycetes: A Handbook of Slime Molds*, Timber Press, Inc., Portland, Oregon.

Summons, R. E., S. C. Brassell, G. Eglinton, E. Evans, R. J. Horodyski, N. Robinson, and D. M. Ward, 1988, Distinctive hydrocarbon biomarkers from fossiliferous sediment of the Late Proterozoic Walcott Member, Chuar Group, Grand Canyon, Arizona, *Geochim. Cosmochim. Acta* **52**: 2625-2637.

Summons, R. E., Thomas, J., Maxwell, J. R., and Boreham, C. J., 1992, Secular and environmental constraints on the occurrence of dinosterane in sediments, *Geochim. Cosmochim. Acta* **56**: 2437-2444.

Summons, R. E., and Walter, M. R., 1990, Molecular fossils and microfossils of prokaryotes and protists from Proterozoic sediments, *Am. J. Sci.* **290-A**: 212-244.

Talyzina, N. M., Moldowan, J. M., Johannisson, A., and Fago, F. J., 2000, Affinities of Early Cambrian acritarchs studied by using microscopy, fluorescence flow cytometry and biomarkers, *Rev. Palaeobot. Palynol.* **108**: 37-53.

Tappan, H., 1980, *The Paleobiology of Plant Protists*, San Francisco.

Tappan, H., 1993, Tintinnids, in: *Fossil Prokaryotes and Protists* (J. H. Lipps, ed.), Blackwell Scientific Publications, Boston, pp. 285-303.

Timofeev, B. V., 1970, Une découverte de phycomycetes dans le Précambrien, *Rev. Palaeobot. Palynol.,* **10**: 79-81.

Versteegh, G. J. M., and Blokker, P., 2004, Resistant macromolecules of extant and fossil microalgae, *Phycol. Res.* **52**: 325-339.

Wang, D., Kumar, S., and Hedges, S., 1999, Divergence time estimates for the early history

of animal phyla and the origin of plants, animals and fungi, *Proc. R. Soc. Lond [Biol.]* **266**: 163-171.

Watters, W. A., and Grotzinger, J. P., 2001, Digital reconstruction of calcified early metazoans, terminal Proterozoic Nama Group, Namibia, *Paleobiology* **27**: 159-171.

Won, M. Z., and Below, R., 1999, Cambrian Radiolaria from the Georgina Basin, Queensland, Australia, *Micropaleontology* **45**: 325-363.

Wood, R. A., Grotzinger, J. P., and Dickson, J. A. D., 2002, Proterozoic modular biomineralized metazoan from the Nama Group, Namibia, *Science* **296**: 2383-2386.

Woods, K. N., Knoll, A. H., and German, T., 1998, Xanthophyte algae from the Mesoproterozoic/Neoproterozoic transition: confirmation and evolutionary implications, *Geol. Soc. Amer. Abstr. Progr.* **30**: A232.

Wylezich, C., Meisterfeld, R., Meisterfeld, S., and Schlegel, M., 2002, Phylogenetic analyses of small subunit ribosomal RNA coding regions reveal a monophyletic lineage of euglyphid testate amoebae (Order Euglyphida). *J. Eukaryot. Microbiol.* **49**: 108-118.

Xiao, S., and Knoll, A. H., 2000, Phosphatized animal embryos from the Neoproterozoic Doushantuo Formation at Weng-An, Guizhou, South China, *J. Paleontol.* **74**: 767-788.

Xiao, S., A.H. Knoll, and X. Yuan, 1998a, Morphological reconstruction of *Miaohephyton bifurcatum*, a possible brown alga from the Neoproterozoic Doushantuo Formation, South China, *J. Paleontol.* **72**: 1072-1086.

Xiao, S., Y. Zhang, and A.H. Knoll, 1998b, Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite, *Nature* **391**: 553-558.

Xiao, S., Yuan, X., Steiner, M., and Knoll, A. H., 2002, Macroscopic carbonaceous compressions in a terminal Proterozoic shale: a systematic reassessment of the Miaohe biota, South China, *J. Paleontol.* **76**: 347-376.

Xiao, S., Knoll, A. H., Yuan, X. L., and Pueschel, C. M., 2004, Phosphatized multicellular algae in the Neoproterozoic Doushantua Formation, China, and the early evolution of the florideophyte algae, *Am. J. Bot.* **91**: 214-227.

Yin, L., 1997, Acanthomorphic acritarchs from Meso-Neoproterozoic shales of the Ruyang Group, Shanxi, China, *Rev. Palaeobot. Palynol.,* **98**: 15-25.

Yoon, H., Hackett, J., Ciniglia, C., Pinto, G., and Bhattacharya, D., 2004, A molecular timeline for the origin of photosynthetic eukaryotes, *Molec. Biol. Evol.* **21**: 809-818.

Yuan, X., Xiao, S., and Taylor, T. N., 2005, Lichen-like symbiosis 600 million years ago, *Science* **308**: 1017-1020.

Zander, J. M., Caspi, E., Pandey, G. N., and Mitra, C., 1969, The presence of tetrahymanol in *Oleandra wallichii*, *Phytochemistry* **8**: 2265-2267.

Zhuravlev, A. Y., 1993, Were Ediacaran Vendobionta multicellulars? *Neues Jahrb. Geol. Paläontol.* **190**(2/3): 299-314.