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Fossil filamentous microorganisms associated with plants in early terrestrial environments

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Microorganisms are ubiquitous in modern environments, where they have a variety of essential functions but little is known about their diversity and roles in early terrestrial environments. The earliest direct evidence of filamentous microorganisms associated with plants occurs around 407 million years ago in landscapes dominated by an herbaceous flora. 100 million years later, forests were well established and associations had increased in diversity. After more than a century since the first descriptions, the need for better understood fossils has renewed interest in their study. New discoveries and advances in imaging methods are beginning to reveal the importance of Cyanobacteria, Fungi and Oomycota and their interactions with plants in early floras.

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Introduction

The first plants colonized Earth's land surfaces in the Ordovician period (ca. 470 Ma) and associations with Cyanobacteria and Fungi are thought to date from this time [1]. However direct fossil evidence of these associations is not visible before 407 Ma and it is very patchy because of the exceptional geological conditions required to preserve cellular and subcellular detail (e.g. rapid permineralization). In this process, once the mineral is precipitated and hardened, the plant material and anything associated with it are entombed in the rock [2]. Special environmental conditions enabled permineralization to occur in Devonian and late Carboniferous cherts (e.g. 407 Ma Rhynie chert, Scotland [3•]; 307 Ma chert of Grand'Croix, France [4] or in carbonate concretions in the late Carboniferous wetlands [5]. Although an important gap separates these two geological periods, they represent privileged paleontological windows to study early plant-microorganism associations. The affinities of fossil microorganisms are determined by comparative morphology (Table 1). The fossil record is largely restricted to sites of exceptional preservation but the available material (including that of sites recently found [6]) is far from being fully investigated and has a great potential to reveal new associations. Today microorganisms are essential components of plant dominated ecosystems acting as symbionts, parasites, or saprotrophs, and a growing body of evidence indicates that they played similar roles in the earliest terrestrial ecosystems. The focus of this review is early filamentous Cyanobacteria, filamentous Fungi and Oomycota with emphasis on their roles in the ecosystems. For this purpose, it covers the period 400–300 Ma. Figure 1 presents a simplified phylogenetic tree showing the plant groups that were present at that time and involved in interactions with microorganisms.

Cyanobacteria — a major component of early plant dominated ecosystems

In the Rhynie chert, the substrate was a thin biological soil crust, formed by bacteria, arthropods, green algae, fungi and putative lichens, on which plants developed [7]; microenvironments ranged from terrestrial to fully freshwater or saline, the salts being derived from hydrothermal vents [8]. Several filamentous forms of Cyanobacteria have been described [9•]. Some developed a heterotrichous thallus and might have grown epiphytically on plant axes [10]. These are currently under reinvestigation (Figure 2a). Others which lack heterocysts are quite common on plant debris and can also be observed within degraded areas of plants (Figure 2b); some of them resemble modern *Oscillatoria* (Figure 2c). One form developed within prostate mycorrhizal axes of the plant *Aglaophyton majus* [11]. The authors suggested that it entered through the stomatal pore (Plate III, Figure 1 in [11], however this is difficult to observe on the image provided) and colonized the substomatal chambers and intercellular spaces of the cortex. Some filaments penetrated cells close to and within the mycorrhizal arbuscule-zone and extended within the cells, but whether these formed symbiotic associations or entered post mortem remains an open question. Cyanobacteria belonging to the genera *Nostoc*, *Stigonema* and *Calothrix* develop nitrogen-fixing symbioses with modern hornworts and some liverworts. They form motile hormogonia, which are essential for successful plant invasion, and heterocysts, which are required for N_2 fixation and the establishment of a functional symbiosis [12]. The fossil

Table 1

Key features for classifying the fossil microorganisms

Microorganisms	Key features	Location	Status	References
Cyanobacteria	Uniseriate filaments of barrel-shaped cells No branching, diameter of the filaments ca. $5\ \mu m$	Prostate mycorrhizal axes of the plant or degraded plant axes	Possibly symbiotic Saprotrophic	[9•] [10]
	Different types of cells in the filament, some resembling heterocysts	Attached to the plant cuticle	Epiphytic	[10]
Chytridiomycota	Reproductive structures (sporangia) located inside or outside the substrate Thalli producing a single reproductive structure or with many centers at which reproductive structures are formed Globose sporangia with discharge papillae Coenocytic hyphae	Algae, fungal spores Structure of unknown affinity	Saprophytic, parasitic Parasitic	[14,16] [15]
Blastocladiomycota	Coenocytic hyphae, thalli with many centers at which reproductive structures are formed Thalli with sympodial branches or dichotomously branched. Lack of septation or pseudoseptation, globose to elongated zoosporangia formed in small clusters Sporangia possibly showing discharge papillae Thick-walled resting reproductive structures	Degraded plant axes Inner cortex of rootlets Among plant debris	Saprophytic Parasitic Saprophytic	[17•] [18] [19•]
Mucoromycotina	Coenocytic hyphae Thin-walled and thick-walled fungal structures in intercellular spaces, intracellular coils	A clear zonation of the fungal colonization in the corm of the plant	Symbiotic	[26•]
	Spore with germination shield, spore with saccule	Within degraded plant axes	Saprophytic	[31,32]
Glomeromycotina	Coenocytic hyphae, sparsely branched Y-shaped and H-shaped anastomoses Division of the plant cell perpendicularly to its main axis Intracellular arbuscules Several layers in the spore walls Subtending hypha closed by invaginated inner layer of the spore wall	Aerial axes of the plant, colonization of the outer cortex	Symbiotic	[22•,23•,26•]
Oomycota	Occurrences of sexual reproductive structures, oogonia with attached antheridia, oosphere. Ornamentation of the oogonia	Microbial mats Plant ovule, periderm of plant, sporangium	Saprotrophic	[36,40]
	Fertilization tube, hyphal attachment Hyphal knots, haustorium	Stem cortex and rootlets	Parasitic	[41•]

association in *Aglaophyton majus* does not fit this type of symbiosis as it is non-heterocystous and hormogonia have not been observed. In contrast, other fossils developed heterotrichous thalli resembling the epiphytic cyanobacteria associated with modern mosses. These could have had a similar role in supplying the combined nitrogen to local ecosystems [12].

Fungi — a great diversity both in terms of organisms and interactions

Zoosporic Fungi (Chytridiomycota and Blastocladiomycota): occurrences linked with the types of environment

Zoosporic Fungi are an early diverging lineage in the fungal tree of life: they comprise at least three phyla, of which two, Chytridiomycota and Blastocladiomycota, develop a range of thallus morphologies [13]. Identifying zoosporic Fungi based on fossil specimens, however, is not straightforward because morphological characters are few and convergent morphologies are found in distantly related eukaryotes such as Hyphochytridiomycota and Oomycota. While several globular forms connected with filaments (rhizoids) from the Rhynie chert have been interpreted as chytrid-like morphotypes or Chytridiomycota (e.g. [14–16]), none of them were directly associated with plants. They occurred in organic rich sediments in wetter parts of the landscape.

The fossil record of Blastocladiomycota is more restricted and all the fossils described to date are associated with plants or plant debris. One species, in which two stages of the life cycle were described [17•] (Figure 2d,e), colonized partially degraded axes of the plant *Aglaophyton majus* where it probably played a saprophytic role. A second similar fungus, with only one stage of the life cycle found, colonized the inner cortex of the small rootlets of the