Archaeorhizomycetes: Unearthing an Ancient Class of Ubiquitous Soil Fungi

Anna Rosling, *et al.*

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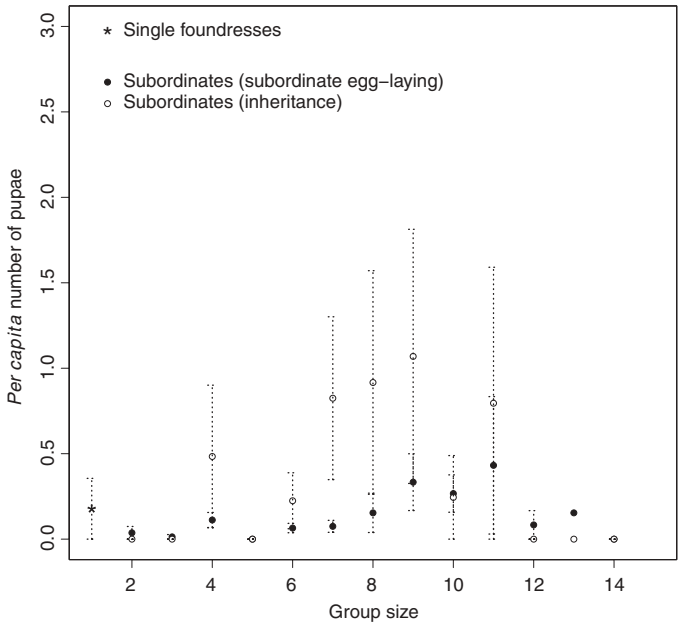

Fig. 3. Subordinate reproductive prospects, through subordinate egg-laying and inheritance, according to group size. Lone foundresses are illustrated for comparison. Error bars, mean ± SEM.

achieve more direct fitness through subordination even to a nonrelative than through nesting alone. However, we do not imply that direct fitness benefits are always the main driver of subordinate behavior, because our data also show that indirect benefits usually outweigh direct benefits for those subordinates [~56 to 70% (*7*, *9*)] that are relatives of the dominant wasp (fig. S3). Rather, direct fitness benefits make subordination worthwhile if wasps either do not have surviving relatives in the population or fail to recognize them. Within our sample, at least 12.8% of unrelated subordinates had sisters that were dominant on nearby nests, suggesting that kin recognition sometimes fails. Individuals should choose to nest with their sisters where possible, but the prospect of nest inheritance means that subordination can be adaptive even when this ideal cannot be achieved.

The importance of inheritance for *P. dominulus* subordinates, even within their short nesting season, means that like helpers in cooperatively breeding vertebrates, their behavior must reflect a trade-off between current (indirect) and future (direct) fitness (*12*, *14*). Inheritance has the potential to stabilize cooperation, because a dominant cannot easily accept help from subordinates, then later renege on the inheritance payoff after her own death (*21*). However, subordinate reproduction will also reduce relatedness between workers and egg-laying foundresses later in the season, helping to explain why a committed altruistic caste has not evolved in *Polistes* (*1*).

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Supporting Online Material

www.sciencemag.org/cgi/content/full/333/6044/874/DC1
Materials and Methods
Figs. S1 to S5
Tables S1 and S2
References (*23*–*33*)

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Archaeorhizomycetes: Unearthing an Ancient Class of Ubiquitous Soil Fungi

Anna Rosling,[1,2*] Filipa Cox,[3] Karelyn Cruz-Martinez,[1] Katarina Ihrmark,[1] Gwen-Aëlle Grelet,[4] Björn D. Lindahl,[1] Audrius Menkis,[1] Timothy Y. James[5*]

Estimates suggest that only one-tenth of the true fungal diversity has been described. Among numerous fungal lineages known only from environmental DNA sequences, Soil Clone Group 1 is the most ubiquitous. These globally distributed fungi may dominate below-ground fungal communities, but their placement in the fungal tree of life has been uncertain. Here, we report cultures of this group and describe the class, Archaeorhizomycetes, phylogenetically placed within subphylum Taphrinomycotina in the Ascomycota. Archaeorhizomycetes comprises hundreds of cryptically reproducing filamentous species that do not form recognizable mycorrhizal structures and have saprotrophic potential, yet are omnipresent in roots and rhizosphere soil and show ecosystem and host root habitat specificity.

Direct sequencing of environmental DNA is a powerful tool to explore cryptic diversity of microorganisms and challenges our understanding of global biodiversity (*1*, *2*). Despite producing macroscopic reproductive structures and being among the largest of eukaryotes (*3*), many fungal species and even phyla have seldom been observed or cultivated (*4*–*6*). Among the lineages known only from environmental DNA sequences, the Soil Clone Group 1 (SCG1) (*5*) is the most common enigmatic lineage in soil (*7*, *8*). The mysterious nature of SCG1 stems from its detection by sequencing in more than 50 ecological studies of soil fungi (tables S1 and S2), but the organisms have never before been observed in the form of fruiting body, spore, culture, or distinctive

[1]Department of Forest Mycology and Pathology, Uppsala BioCentre, SLU, Box 7026, 750 07 Uppsala, Sweden. [2]Department of Biology, Indiana University, Bloomington, IN 47405, USA. [3]Imperial College London and Royal Botanic Gardens, Kew, London TW9 3DS, UK. [4]The University of Aberdeen and James Hutton Institute, Aberdeen AB24 3UU, UK. [5]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA.

*To whom correspondence should be addressed. E-mail: anna.rosling@slu.se (A.R.); tyjames@umich.edu (T.Y.J.)

mycorrhizal morphotype. Moreover, its uncertain placement within the Ascomycetes based on analysis of ribosomal RNA (rRNA) gene sequences from soil DNA extracts did not provide a phylogenetic association with previously described fungi. Because it has never been detected in root-free environmental samples, SCG1 was hypothesized to be obligately biotrophic (*5*).

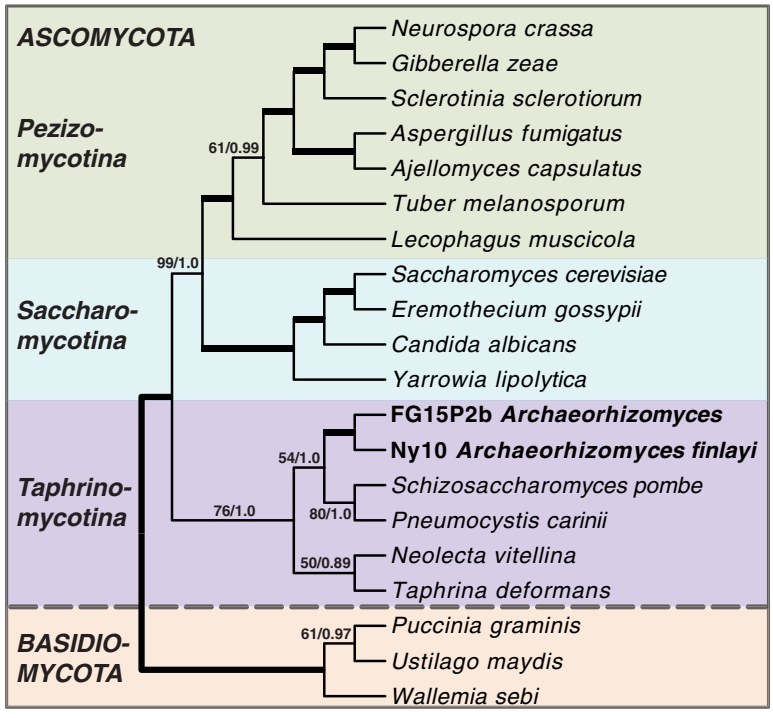

Fig. 1. Consensus phylogeny of Fungi, showing the placement of *Archaeorhizomyces* based on the combined gene data set. Shown is the consensus tree across bootstrap pseudo-replicates for a partitioned data set (nucleotides and amino acids) estimated by maximum likelihood (ML) with Garli 2.0 (*34*). Shown at nodes are the frequencies of bootstrap replicates in the partitioned ML analysis followed by Bayesian posterior probability (partitioned analysis). Thickened nodes are supported by 100% bootstrap followed by posterior probability.

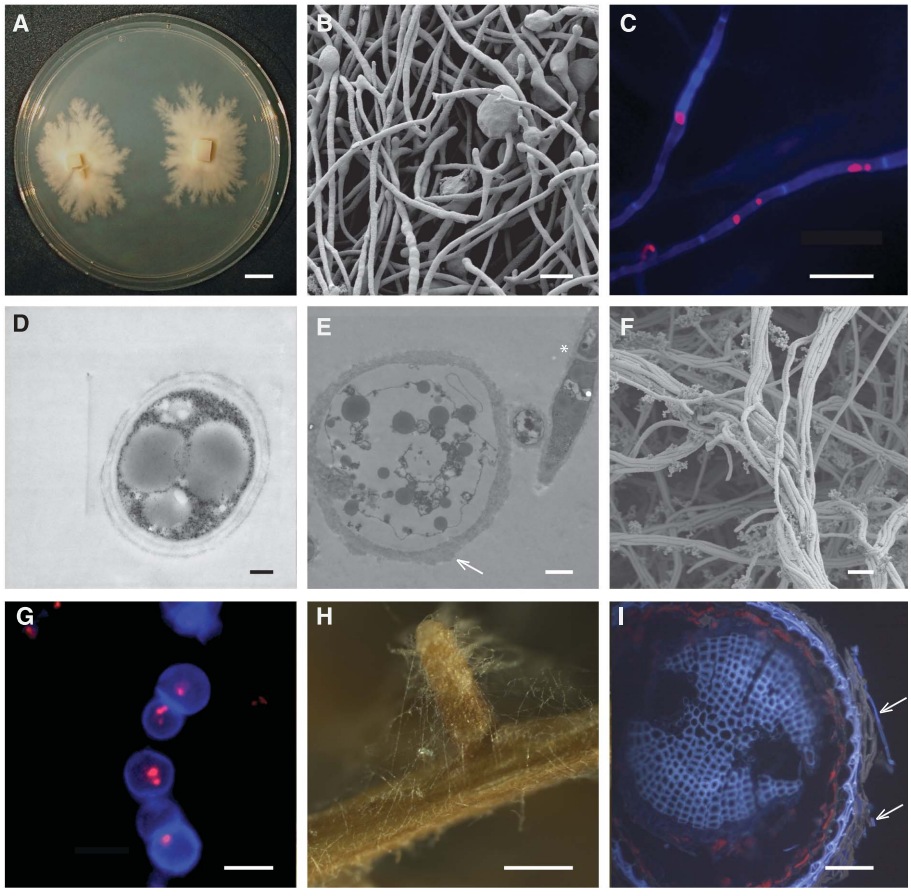

Fig. 2. *A. finlayi* is the type species in the Archaeorhizomycetes. (**A**) Six-month-old culture growing on MMN agar. (**B**) Scanning electron micrograph (SEM) image of fixed mycelia from 3-month-old mycelia with both terminal and intercalary swellings. (**C**) Six-month-old mycelia stained with calcofluor white and propidium iodide. (**D**) Transmission electron micrograph (TEM) cross section of hyphae in 3-month-old mycelia. (**E**) TEM cross section of swelling and septate hyphae (*) in 3-month-old mycelia with extensive coating in extracellular material (arrow). (**F**) SEM image of aerial cord-like structure in 3-month-old mycelia. (**G**) Chlamydospore-like hyphal swellings contain one to several nuclei, prepared as in (C). (**H**) *A. finlayi* grown for 6 months in association with pine roots under sterile conditions. (**I**) Cryostat cross section of colonized pine root stained with calcofluor white, septate hyphae on the root surface (arrowed). Scale bars: 1 cm (A), 0.5 mm (H), 25 μm (I), 10 μm (C and G), 5 μm (B and F), 1 μm (E), and 200 nm (D).

Here, we characterize cultures of SCG1 (*9*) isolated as slow-growing fungi emerging from surface-sterilized coniferous ectomycorrhizal root tips (*10*, *11*). Initial species identification based on the rapidly evolving internal transcribed spacer (ITS) rRNA locus did not allow phylogenetic placement of the isolates, and only after sequencing a larger, 3.6-kbp rRNA locus fragment were the isolates rediscovered as the SCG1. The availability of cultures allowed a robust and reliable multilocus phylogenetic assessment with unambiguous linkage relationships among rRNA genes and three protein-coding genes (*9*), an approach not possible with environmental DNA. We propose the class Archaeorhizomycetes, which is diagnosable with rRNA sequences, and describe the type species *Archaeorhizomyces finlayi* (*12*–*16*).

Archaeorhizomycetes is placed within the subphylum Taphrinomycotina in the combined gene analysis and in separate analyses of two out of three protein-coding genes (Fig. 1 and fig. S1). Modest support in the combined gene phylogeny (Fig. 1) is likely due to conflict between rRNA and protein-coding genes and the ancient divergence time of the Taphrinomycotina. However, Archaeorhizomycetes is part of a monophyletic or paraphyletic Taphrinomycotina in every single locus phylogeny (fig. S1), and the monophyly of Taphrinomycotina has been statistically supported in other studies (*17*–*19*). Taphrinomycotina includes four distinct classes that encompass extreme phylogenetic and ecological diversity despite containing only six genera and 150 species (*19*, *20*). Taphrinomycotina includes the model fission yeast *Schizosaccharomyces*, the mammal pathogen *Pneumocystis* associated with HIV patients, and the enigmatic genus *Neolecta*. *Neolecta* grows attached to rootlets of conifers, is the only Taphrinomycotina known to produce fruiting bodies, and has not yet been cultured (*21*, *22*).

A. finlayi is a slow-growing mycelial fungus (Fig. 2A) with thin hyphae (1 to 2 μm) (Fig. 2, B to D) and simple septa without pores (Fig. 2, C and E, and fig. S2, A and B). The hyphal cell wall is double layered and ~200 nm thick (Fig. 2D). In culture, the hyphae are extensively coated by extracellular material (Fig. 2E) and intertwined into undifferentiated cord-like structures (Fig. 2F). Cells have one or often multiple nuclei (Fig. 2C). Both terminal and intercalary swellings are observed (Fig. 2, B and E) and delimited by septa. The swellings are typically thick-walled and contain multiple nuclei (Fig. 2, E and G), suggesting that they may function as resistant spores (chlamydospores).

Direct sequencing of the rRNA ITS locus from root tips has identified members of Archaeorhizomycetes from 2.2 to 3.5% of all examined root tips of *Betula nana* (*23*), *Pinus sylvestris* (*24*, *25*), and *Picea abies* (*25*). This is despite the fact that all Archaeorhizomycetes sequences have two specific mismatches (*15*) in the binding site of the widely used reverse primer ITS4 (*26*). In contrast, when the large subunit (LSU) rRNA gene was used as a marker, 7 to 95% of cloned amplicons were ascribed to Archaeorhizomycetes in different soil habitats (*5*, *7*, *27*). Similarly, 19% of small subunit (SSU) rRNA gene sequences belonged to Archaeorhizomycetes, despite the same soil DNA extract yielding zero amplified Archaeorhizomycetes ITS sequences (*28*). Hence, species in the Archaeorhizomycetes may be far more abundant than suggested from the majority

OTU	Distribution	Habitat
1.	British Columbia	Tsuga roots
2.	North hemisphere	broad
3.	North hemisphere	Picea roots
4.	North America	broad
5.	Europe	Pinus, Ericaceae
6.	North hemisphere	Pinus, Ericaceae
7.	North hemisphere	broad
8.	North America	Hardwood
9.	North hemisphere	broad
10.	Europe	Pinus
11.	Scandinavia	Conifer
12.	North hemisphere	broad
13.	North hemisphere	Picea, Ericaceae
14.	North America	Hardwood

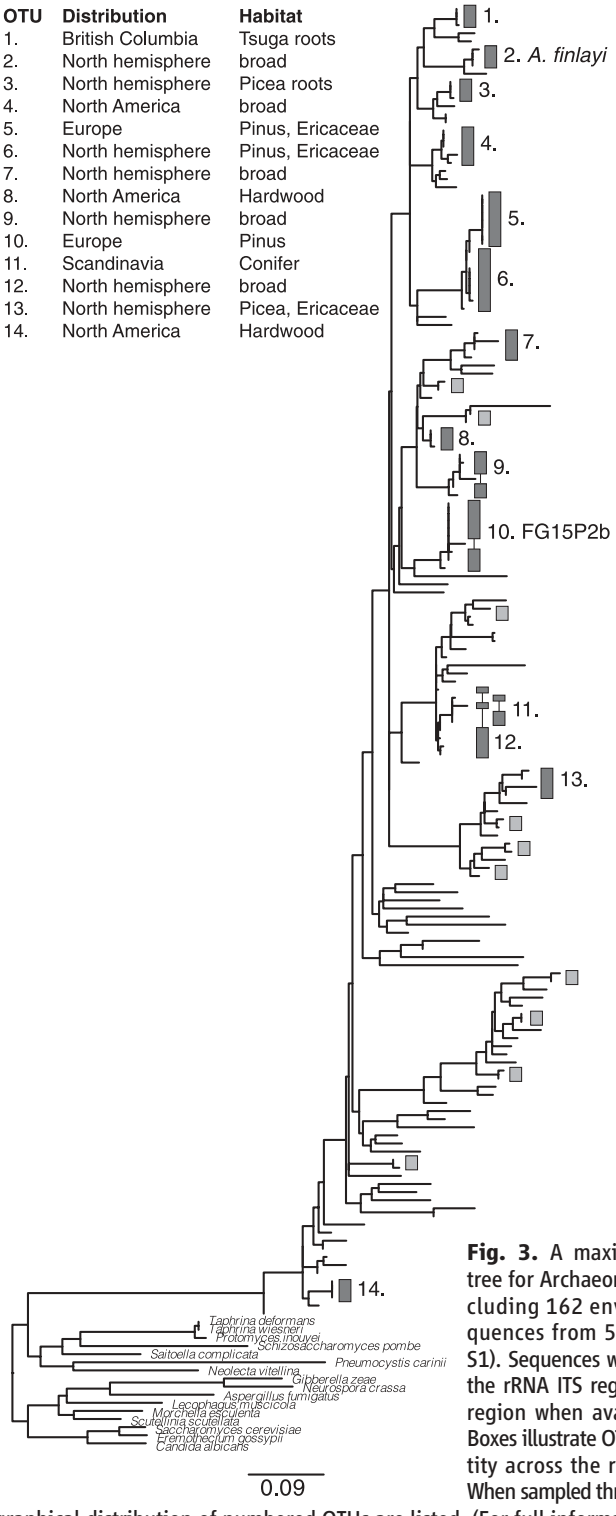

Fig. 3. A maximum likelihood tree for Archaeorhizomycetes, including 162 environmental sequences from 52 studies (table S1). Sequences were aligned over the rRNA ITS region and the 28*S* region when available (fig. S4). Boxes illustrate OTUs at 97% identity across the rRNA ITS region. When sampled three times or more, habitat and geographical distribution of numbered OTUs are listed. (For full information, see fig. S3 and table S1). *A. finlayi* is the type species in this class, and FG15P2b represents a culture from an additional unnamed species. Outgroups are aligned across 28*S* and 5.8*S*. The scale bar indicates substitutions per site.

of molecular community studies, which have used the mismatching ITS4 primer (*26*).

In a meta-analysis of publicly available ITS and LSU sequences (figs. S3 and S4), we distinguished at least one hundred operational taxonomic units (OTUs, roughly equivalent to species) of Archaeorhizomycetes, using a 97% sequence similarity threshold across the ITS region (Fig. 3), and predicted a total diversity exceeding 250 OTUs (*9*) (fig. S5). We confirmed previous observations of high local diversity, with 12 to 20 OTUs per site (*5*, *27*). Furthermore, we demonstrated strong biogeographical patterns, with significant global association between geographic and phylogenetic distance (Mantel $R = 0.201$, $P = 0.0001$; fig. S6). Globally distributed OTUs were associated with specific ecosystems and habitats (Fig. 3) (SOM text). The three most sampled OTUs (number 5, 6, and 10 in Fig. 3) colonize typical ectomycorrhizal habitats—i.e., soil and roots of pine and understory ericaceous plants. However, there is no evidence that Archaeorhizomycetes form mycorrhizal structures in pine roots. Instead, Archaeorhizomycetes sequences have been amplified from distinct ectomycorrhizal morphotypes (*10*, *11*, *29*–*31*), where they commonly coexist with other fungi in single root tips (*10*, *29*, *32*). When inoculated onto sterile pine seedlings, the mycelium of *A. finlayi* associates with roots but shows no preferential growth toward main, primary, or secondary roots and does not alter root tip morphology (*9*) (Fig. 2H). Despite a lack of typical mycorrhizal or endophytic structures (Fig. 2I), inoculated seedlings remained healthy for months, with no signs of fungal pathogenicity. The apparent plant host and habitat specificity demonstrated by many OTUs is not necessarily explained by specificity toward the plant, but may instead reflect an association with other root-associated fungi.

When first discovered, Archaeorhizomycetes were found to be seasonal, dominating tundra soil fungal communities in summer while being absent during other times of the year (*7*). This suggests that these fungi depend on root-derived carbon compounds. However, in culture, *A. finlayi* grows slowly on both glucose and cellulose as a sole carbon source (*9*) (fig. S7), indicating that it may be involved in decomposition and not require direct carbon transfer from the plant through symbiosis.

The diverse fungal class Archaeorhizomycetes occurs ubiquitously in different terrestrial ecosystems, and so far their abundance has been underestimated owing to amplification biases. Although their precise ecological niches and their complete life cycle remain unknown, the isolation and description of cultures of this group will allow their role in terrestrial ecosystems to be deciphered by in vitro characterization and genome sequencing. Like the recently described aquatic lineage cryptomycota (*6*), these observations of Archaeorhizomycetes contribute toward cataloging and understanding the missing diversity of the fungal kingdom (*33*). Their cryptic nature and recalcitrance to culture may explain why these dominant forms of the biosphere remained undetected until the onset of environmental DNA studies.

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12. Archaeorhizomycetes Rosling and T. James class nov. **Etymology:** from Greek arkhaio-, ancient; referring to the basal placement of the genus within the Ascomycota; from Greek rhiza referring to roots; Greek mykes referring to fungi. *Cum Taphrinomycotina phylogenetice locatae, sed differt incremento myceliali in agaro una cum radicibus plantarum vivarum. Characteres moleculares distincti: Loci LSU: (AACAAGTAG) comparati Saccharomyces cerevisiae (M19229.1: 347-355) et SSU: (T) comparati S. cerevisiae (Z75578: 883).* **Genus typica:** *Archaeorhizomyces* Rosling and T. James. **Translation of diagnosis:** Phylogenetically placed among Taphrinomycotina, differing by mycelial growth on MMN agar together with an association with roots of living plants. Distinctive molecular characters: LSU: (AACAAGTAG) positions relative to *Saccharomyces cerevisiae* (M19229.1: 347-355) and SSU: (T) positions relative to *S. cerevisiae* (Z75578: 883). Synonymous to Soil Clone Group 1 (SCG1) (*5*).
13. Archaeorhizomycetales ord. nov. *descriptio ad genus.* **Genus typica:** *Archaeorhizomyces* Rosling and T. James.
14. Archaeorhizomycetaceae fam. nov. *descriptio ad genus*. **Genus typica:** *Archaeorhizomyces* Rosling and T. James.
15. *Archaeorhizomyces* Rosling and T. James, gen. nov. *Coloniae in MMN agaro albae usque ad luteas, tarde crescentes et plumeae. Partim per LSU et 5.8 rDNA cognitae. Telemorphus incognitus. Genus serie rDNA distinctum: Loci 5.8S: (A) pro ratione cum Saccharomyces cerevisiae (K01048.1: 14) et loci LSU: (GCATATCAATAAGGYGAGGA) pro ratione cum Saccharomyces cerevisiae (M19229.1: 40-59).* **Species typica:** *Archaeorhizomyces finlayi* Rosling & T. James. **Translation of description:** Colonies on MMN agar creamy-white to yellowish white; slow growing and appearing feathery. Teleomorph unknown. Distinguished by sequencing of the rDNA 5.8S: (A) position relative to *Saccharomyces cerevisiae* (K01048.1: 14) and LSU: (GCATATCAATAAGGYGAGGA) positions relative to *Saccharomyces cerevisiae* (M19229.1: 40–59), the ITS4 primer binding site. **Distribution:** Cosmopolitan distribution in roots and rhizosphere soil. Fig. 3.
16. *Archaeorhizomyces finlayi* Rosling and T. James sp. nov. **Etymology:** *finlayi*; in honor of Prof. Roger D. Finlay at SLU, Uppsala, Sweden, for his many contributions to rhizosphere ecology. *Consocciatus cum radicibus aborum coniferarum. Coloniae in MMN mediis hydrophilae sunt hyphis paucis aeriis et morphologia sicut plumae in margine prima. Mycelium e hyphis tenuibus compositum (1-2 μm diametro), septis simplicibus poros carentibus. Hyphae materia extracellulari tectae. Maturitate chlamydosporas (3-6 μm diametro) 1- 4 haphis emergentibus faciens. Distinct characteribus ITS: (TTTGGCGCCCGGTCTATGCC) loci pro ratione cum GenBank JF836021: 60-79.* **HOLOTYPUS:** MICH72671, a dried culture on MMN, isolated from a surface sterilized ectomycorrhizal root tip collected in mixed coniferous forest in the north of Sweden (Nyänget, 64°15′ N, 19°45′ E), in August 1999. (MICH). Ex holotype culture CBS 128710 = UPG613-Ny9. Other concomitantly isolated strains examined UP605-Ny14, UP606-Ny10. **Translation of description:** Associated with roots of coniferous trees. Colonies on MMN media are hydrophilic with minimum aerial hyphae and have a feathery leading-edge morphology. Mycelium comprised of thin hyphae (1 to 2 μm in diameter) with simple septa lacking pores. Hyphae are coated in extracellular material. With age producing chlamydospores (3 to 6 μm in diameter) with up to four emerging hyphae. Possessing the following distinctive ITS characters: (TTTGGCGCCCGGTCTATGCC) positions relative to GenBank JF836021: 60–79. **Distribution:** Scandinavia and North America. **Molecular characters**: ITS sequences of three strains considered *A. finlayi* are 100% identical (JF836021, DQ233781, HQ022034).
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Supporting Online Material

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Materials and Methods
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Figs. S1 to S7
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References (*35*–*72*)

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