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A phylogeny of the highly diverse cup-fungus family Pyronemataceae (Pezizomycetes, Ascomycota) clarifies relationships and evolution of selected life history traits

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ABSTRACT

Pyronemataceae is the largest and most heterogeneous family of Pezizomycetes. It is morphologically and ecologically highly diverse, comprising saprobic, ectomycorrhizal, bryosymbiotic and parasitic species, occurring in a broad range of habitats (on soil, burnt ground, debris, wood, dung and inside living bryophytes, plants and lichens). To assess the monophyly of Pyronemataceae and provide a phylogenetic hypothesis of the group, we compiled a four-gene dataset including one nuclear ribosomal and three protein-coding genes for 132 distinct Pezizomycetes species (4437 nucleotides with all markers available for 80% of the total 142 included taxa). This is the most comprehensive molecular phylogeny of Pyronemataceae, and Pezizomycetes, to date. Three hundred ninety-four new sequences were generated during this project, with the following numbers for each gene: RPB1 (124), RPB2 (99), EF-1 α (120) and LSU rDNA (51). The dataset includes 93 unique species from 40 genera of Pyronemataceae, and 34 species from 25 genera representing an additional 12 families of the class. Parsimony, maximum likelihood and Bayesian analyses suggest that Pyronemataceae is paraphyletic due to the nesting of both Ascodesmidaceae and Glaziellaceae within the family. Four lineages with taxa currently classified in the family, the *Boubovia*, *Geopyxis*, *Pseudombrophila* and *Pulvinula* lineages, form a monophyletic group with Ascodesmidaceae and Glaziellaceae. We advocate the exclusion of these four lineages in order to recognize a monophyletic Pyronemataceae. The genus *Coprotus* (Thelebolales, Leotiomyces) is shown to belong to Pezizomycetes, forming a strongly supported monophyletic group with *Boubovia*. Ten strongly supported lineages are identified within Pyronemataceae s. str. Of these, the *Pyropyxis* and *Otidea* lineages are identified as successive sister lineages to the rest of Pyronemataceae s. str. The highly reduced (gymnohymenial) *Monascella* is shown to belong to Pezizomycetes and is for the first time suggested to be closely related to the cleistothecial *Warcupia*, as a sister group to the primarily apothecial *Otidea*. None of the lineages of pyronemataceous taxa identified here correspond to previous families or subfamily classifications. Ancestral character state reconstructions (ASR) using a Bayesian approach support that the ancestors of Pezizomycetes and Pyronemataceae were soil inhabiting and saprobic. Ectomycorrhizae have arisen within both lineages A, B and C of Pezizomycetes and are suggested to have evolved independently seven to eight times within Pyronemataceae s. l., whereas an obligate bryosymbiotic lifestyle has arisen only twice. No reversals to a free-living, saprobic lifestyle have happened from symbiotic or parasitic Pyronemataceae. Specializations to various substrates (e.g. burnt ground and dung) are suggested to have occurred several times in mainly saprobic lineages. Although carotenoids in the apothecia are shown to have arisen at least four times in Pezizomycetes, the ancestor of Pyronemataceae s. str., excluding the *Pyropyxis* and *Otidea* lineages, most likely produced carotenoids, which were then subsequently lost in some clades (– and possibly gained again). Excipular hairs were found with a high probability to be absent from apothecia in the deepest nodes of Pezizomycetes and in the ancestor of Pyronemataceae s. str. True hairs are restricted to the core group of Pyronemataceae s. str., but are also found in *Lasiobolus* (Ascodesmidaceae), the *Pseudombrophila* lineage and the clade of Chorioactidaceae, Sarcoscyphaceae and Sarcosomataceae. The number of gains and losses of true hairs within Pyronemataceae s. str., however, remains uncertain. The ASR of ascospore guttulation under binary coding (present or absent) indicates that this character is fast evolving and prone to shifts.

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1. Introduction

Pezizomycetes, commonly known as cup-fungi or operculate discomycetes, are among the earliest diverging lineages of Pezizomycotina (the largest subphylum of the Ascomycota) along with Orbiliomycetes (Spatafora et al., 2006; Schoch et al., 2009). The class currently includes 1684 species (Kirk et al., 2008), classified in 16 families and a single order, Pezizales. With the exception of two families with several members in the tropics, cup-fungi are most diverse in temperate regions or at high elevations. They are saprobic, mycorrhizal/symbiotic and a few are plant parasitic. A shared derived character, the operculate ascus (a lid-like structure at the apex of the asci that opens at spore discharge), characterizes Pezizomycetes. Pyronemataceae is the largest and most heterogeneous family of Pezizales, with 78 genera that encompass ca. 660 currently recognized species (Kirk et al., 2008). The family is highly diverse both morphologically and ecologically. Species produce fruitbodies (ascmata) that are epigeous, sessile to stipitate or rooting, disc-, cup- or ear-shaped (apothecia) and with active spore dispersal, or sub-hypogeous to hypogeous, closed, folded to solid and without active spore dispersal (i.e., truffles) (Fig. 1). The fruitbodies range in size from 300 μm to 12 cm in diam. Until recently, most epigeous fruiting Pyronemataceae have been considered primarily saprobic and rarely plant pathogenic, but an increasing number of species are being identified as ectomycorrhizal associates using molecular techniques (e.g. Smith et al., 2007; Tedersoo et al., 2006, in press), i.e. they live in a mutualistic symbiosis with plant roots; they gain photosynthetic sugars from their plant hosts, which in turn benefit from fungus-mediated uptake of mineral nutrients. Furthermore several groups of Pyronemataceae have been found as orchid associates (Tešitelov et al., 2012; Waterman et al., 2011), or as foliar endophytes and endolichenic (U'Ren et al., 2010), i.e. they live within asymptomatic aboveground living tissues such as plant leaves and lichen thalli (close to the photobiont), respectively. Species of Pyronemataceae occur in a broad range of habitats and many are substrate specialists, fruiting on all types of soil, including burnt ground, on dung, decaying leaves, needles, wood and living mosses. The majority of the soil-inhabiting species have a preference for high pH and a low content of organic matter (Petersen, 1985) and often produce ascmata in disturbed habitats. The family is primarily temperate to arctic-alpine in distribution, but a few strictly tropical taxa are known.

No shared derived characters define Pyronemataceae. It has been a default family for pezizalean taxa with uninucleate spores and iodine negative asci that lack distinguishing anatomical characters by which they could be segregated into natural families. Most other families of Pezizomycetes are now considered quite well delimited and are recognized, or have been refined, primarily by using characters such as: the number of nuclei in the ascospores; ascus apical ultrastructure and histochemistry; ultrastructure of the septal pore plug located at the base of the asci and in the ascogenous hyphae; and molecular data (see van Brummelen, 1994; Kimbrough, 1994; Hansen and Pfister, 2006; Læssøe and Hansen, 2007; Pfister et al., 2008; Hansen et al., 2008). Pyronemataceae share the presence of uninucleate spores with Ascobolaceae and Pezizaceae, but lack the blueing reaction of the asci in iodine solutions unique to these two families. Distinctive septal pore plugs in the asci and ascogenous hyphae characterize most families of Pezizomycetes, but within Pyronemataceae at least five distinct types have been reported (Kimbrough, 1994). The lack of clear synapomorphies is reflected in the concept of Pyronemataceae that has varied widely among contemporary mycologists. Some authors included only one or two genera (Arpin, 1969; Rifai, 1968; Kimbrough, 1970) while others included from 21 (Eckblad, 1968) to 49 genera (Korf, 1972, 1973). When the Pyronemataceae is used in a restricted sense, the families Aleuriaceae *sensu* Arpin (1969),

Otidea, Humariaceae and Ascodesmidaceae have been employed to accommodate the remaining taxa.

When the concept of Pyronemataceae was first expanded, the inability to satisfactorily subdivide the family on common characters was indicated (Eckblad, 1968). Consequently it was accepted as a taxon characterized by very wide, but continuous patterns of variation in a few characters, such as spore ornamentation, excipulum structure and type of excipular hairs. Three distinct phylogenetic lines were delineated, but these were recognized by a gradual transition of the characters from one line to the other (Eckblad, 1968). Carotenoid pigments in the apothecia were regarded as the principal character of the family, although several genera with hyaline paraphyses (*Humaria*, *Leucoscypha*, *Geopora*, *Pseudombrophila*, *Sphaerosporella*, *Tricharina*, *Trichophaea*) were regarded as derived within the family. The family Otidea was erected for genera that produce larger, sometimes stipitate apothecia, most of which typically lack bright orange to red coloration: *Ascosparsis*, *Geopyxis*, *Otidea*, *Sowerbyella* and *Tarzetta* (Eckblad, 1968).

One formal subfamily level classification for a broadly defined Pyronemataceae has been proposed (Korf, 1972). It includes five subfamilies, Pyronematoideae, Ascophanoideae, Ascodesmidoideae, Otideoideae and Scutellinioideae, and eleven tribes. The divisions into subfamilies (Korf, 1972, 1973) or families (Arpin, 1969; Kimbrough, 1970) were based primarily on the pigmentation of the apothecia (\pm carotenoids), spore pigmentation and guttulation, and the presence or absence of a subiculum. The divisions into tribes (Korf, 1972) were further based on characters such as presence or absence, origin and pigmentation of apothecial hairs (\pm rooting, \pm pigmented). Hypogeous taxa (truffles) were transferred to Pyronemataceae *sensu* Korf, when the strictly hypogeous, polyphyletic order Tuberales, was abandoned (see Læssøe and Hansen, 2007).

Based on ascumatal ontogeny, type of operculum development and distinctive striated septal pore plugs in the base of the asci, Kimbrough (1989, 1994) argued for a restricted concept of the Pyronemataceae, including only *Pyronema* and *Coprotus* (Fig. 1a and b). Following this, Korf and Zhuang (1991) placed numerous other taxa once treated in the family (not including Ascodesmidaceae and Thelebolaceae) in two subfamilies of the Otidea, Otideoideae and Scutellinioideae, using the presence or absence of carotenoids and hairs of the apothecia. Molecular phylogenetic studies (Hansen and Pfister, 2006; Liu and Zhuang, 2006; Perry et al., 2007) have not supported a segregation of *Pyronema* from the Otidea. Nevertheless, LSU and SSU rDNA sequences of *Pyronema* appeared to be somewhat divergent, as did sequences of such genera as *Otidea* and *Sowerbyella*, and the sister group relationships of *Pyronema* is still unresolved. For a further review of the taxonomic history of Pyronemataceae see Perry et al. (2007).

Molecular phylogenetic analyses have identified three main lineages within Pezizomycetes. The Pyronemataceae in all analyses is nested within a strongly supported C lineage (e.g. Landvik et al., 1997; Hansen and Pfister, 2006; Marek et al., 2009), along with the families Ascodesmidaceae, Chorioactidaceae, Glaziellaceae, Sarcoscyphaceae and Sarcosomataceae. In all of these previous analyses, the relationships among the families within the C lineage were not recovered with strong support. In our previous molecular phylogenetic study of Pyronemataceae (Perry et al., 2007), we included a significant number of taxa (201 Pezizomycetes species) and employed the large subunit nuclear ribosomal RNA gene (LSU-rDNA), spanning domains D1 and D2. The results indicate that Pyronemataceae, in its broad circumscription, does not represent a monophyletic family, due to the nesting of Ascodesmidaceae within, and the resolution of several pyronemataceous taxa outside, the family. Additionally, placement of the monotypic Glaziellaceae within Pyronemataceae could not be rejected. Fourteen primary clades of pyronemataceous taxa were identified, but the relationships among these were not supported using only LSU

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