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Phylogeny of rock-inhabiting fungi related to Dothideomycetes


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Abstract: The class Dothideomycetes (along with Eurotiomycetes) includes numerous rock-inhabiting fungi (RIF), a group of ascomycetes that tolerates surprisingly well harsh conditions prevailing on rock surfaces. Despite their convergent morphology and physiology, RIF are phylogenetically highly diverse in Dothideomycetes. However, the positions of main groups of RIF in this class remain unclear due to the lack of a strong phylogenetic framework. Moreover, connections between rock-dwelling habit and other lifestyles found in Dothideomycetes such as plant pathogens, saprobes and lichen-forming fungi are still unexplored. Based on multigene phylogenetic analyses, we report that RIF belong to Capnodiales (particularly to the family Teratosphaeriaceae s.l.), Dothideales, Pleosporales, and Mynangiellales, as well as some uncharacterised groups with affinities to Dothideomycetes. Moreover, one lineage consisting exclusively of RIF proved to be closely related to Arthoniomycetes, the sister class of Dothideomycetes. The broad phylogenetic amplitude of RIF in Dothideomycetes suggests that total species richness in this class remains underestimated. Composition of some RIF-rich lineages suggests that rock surfaces are reservoirs for plant-associated fungi or saprobes, although other data also agree with rocks as a primary substrate for ancient fungal lineages. According to the current sampling, long distance dispersal seems to be common for RIF. Dothideomycetes lineages comprising lichens also include RIF, suggesting a possible link between rock-dwelling habit and lichenisation.

Key words: Arthoniomycetes, Capnodiales, Dothideomycetes, evolution, extremotolerance, multigene phylogeny, rock-inhabiting fungi.

INTRODUCTION

The Dothideomycetes constitute the largest class of ascomycetes with approximately 19 000 species, which are currently classified in 11 orders and 90 families (Kirk et al. 2008). This class is ecologically diverse, with many pathogens or saprobes on plants, some coprophilous species, and a few lichen-forming fungi (Schoch et al. 2009b; this volume). Early studies have shown that a large part of the non-lichenised, slow-growing melanised fungi isolated from rock surfaces (here referred to as rock-inhabiting fungi) also belong to this class (Sterflinger et al. 1997, 1999). Subsequent sampling efforts revealed a higher diversity of species than expected for these rock-inhabiting fungi (Ruibal 2004, Ruibal et al. 2005, 2008, Selbmann et al. 2005, 2008).

Rock-inhabiting fungi (RIF) are peculiar organisms that apparently lack sexual reproductive structures and form compact, melanised colonies on bare rock surfaces (Fig. 1). Although very common, RIF have often been overlooked due to their small size, their slow growth and the lack of diagnostic features. First discovered in hot and cold deserts (Krumbein & Jens 1981, Friedmann 1982, Staley et al. 1982), RIF are now known to be ubiquitous on hard surfaces, in extreme as well as in temperate climates (Urzi et al. 1995, Sterflinger & Prillinger 2001, Gorbushina 2007, Gorbushina & Broughton 2009). RIF are well adapted to nutrient-poor and dry habitats where they are particularly successful colonisers due to restricted competition with other microbes (Gorbushina 2007) and their extremotolerance.

Extremotolerance comprises some specific universally present adaptations that enable these fungi to tolerate surprisingly wide ranges of temperatures, irradiation and osmotic stresses (Palmer et al. 1990, Sterflinger 1998, Gorbushina et al. 2003, Ruibal 2004, Onofri et al. 2007, Gorbushina et al. 2008). Melanisation protects cells against UV radiations (Dadachova & Casadevall 2008), whereas the typical isodiametrical (meristematic) growth form ensures an optimal volume : surface ratio and, therefore, allows them to survive extreme temperatures and desiccation (Wollenzen et al. 1995). These oligotrophic organisms are able to rely only on sparse, airborne nutrients available on rock surfaces. Their growth on these substrates is limited, and, for some of them, the production of internal asexual spores further allows to save energy. All adaptations contribute to the amazing survival capabilities of RIF in hostile habitats. The environmental tolerance of these fungi, and, in some cases, their capacity to penetrate minerals, make them an attractive subject for studies in microbial ecophysiology and applied research, such as biodeterioration of monuments and exobiology (Gorbushina et al. 1993, Diakumaku et al. 1995, Wollenzen et al. 1997, Gorbushina et al. 2002, Gorbushina 2003, Onofri et al. 2008).

Sterflinger et al. (1997) provided the first molecular evidence of RIF phylogenetic affiliations, and they are known to belong to two groups of ascomycetes, namely Dothideomycetes and Eurotiomycetes (de Hoog et al. 1999, Sterflinger et al. 1999, Ruibal 2004, Ruibal et al. 2005, 2008, Sert et al. 2007a). In Eurotiomycetes, multigene phylogenetic analyses have shown that
RIF cluster in early diverging lineages of Chaetothyriales, whereas two species seem to be more closely related to the lichenised order Verrucariales, the sister group of Chaetothyriales (Gueidan et al. 2008). Gueidan et al. (2008) also demonstrated that the most recent common ancestor of both lichenised Verrucariales and pathogen-rich Chaetothyriales was probably a rock-inhabiting fungus. It was hypothesised that adaptations to life in extreme conditions might have been a prerequisite for the evolution of human pathogenicity (de Hoog 1993, Haase et al. 1999, Gueidan et al. 2008) and lichenisation in this class (Gueidan et al. 2008). In contrast, despite the high diversity of RIF within Dothideomycetes, only very few human pathogens are known from this class of Ascomycota (de Hoog et al. 2000). Alternatively, associations with plants and in particular plant pathogenicity are very common (Schoch et al. 2006, Arzanlou et al. 2007, Crous et al. 2007a–c, 2009; this volume). Additionally, lichenised species also appeared to be nested within Dothideomycetes (Lutzoni et al. 2004, James et al. 2006, Del Prado et al. 2006, Muggia et al. 2008, Nelsen et al. 2009).

Presently no strong phylogenetic hypothesis is available to assess the placement of RIF within Dothideomycetes. Moreover, no studies have investigated phylogenetic relationships among RIF, lichen-forming fungi and plant-associated fungi within Dothideomycetes. Our main goal was to infer phylogenetic relationships of RIF within Dothideomyceta, a lineage including Dothideomycetes and Arthoniomycetes, to explore more specifically their diversity, origins and evolution.

MATERIAL AND METHODS

Taxon and gene sampling

Representative taxa of most of the main orders and families of Dothideomyceta (Dothideomycetes and Arthoniomycetes) were sampled. Two separate sets of data matrices were assembled. The first set (three-gene analysis; Table 1 in Supplementary Information) is composed of 182 taxa (including 102 rock-inhabiting strains) for which DNA sequences of three ribosomal genes have been obtained: the large and second largest subunits of the nuclear ribosomal RNA gene (nucLSU and nucSSU, respectively) and the small subunit of the mitochondrial ribosomal RNA gene (mtSSU). Because this first set of data matrices included only ribosomal genes, low phylogenetic confidence was expected for deep relationships within Dothideomyceta. To overcome this problem, a second set of data matrices was assembled (five-gene analysis; Table 1 in Supplementary Information) consisting of DNA sequences of five loci from 113 taxa (including 40 rock-inhabiting strains): the largest and second largest subunits of the RNA polymerase II (RPB1 and RPB2, respectively), nucLSU, nucSSU and mtSSU. The outgroup for the three-gene analysis included Hyphozyma lignicola, Symbiotaphrina buchneri and S. kochii, whereas only the latter two species were selected as outgroup for the five-gene analysis. These species were chosen because they constituted a sister group to Dothideomyceta in a previous study (Schoch et al. 2009a).

DNA isolation and sequencing

Different laboratories contributed data using various protocols, but most DNA sequence information was produced as follows: genomic DNA was isolated from cultures grown on MEA. Fungal biomass was transferred to a tube with 500 µL of TES buffer and ground with a micro-pestle for 1–2 min, with or without silica-mix (2/3 silica-gel, 1/3 Celite® 545). A volume of 140 µL of 5 M NaCl was then added, followed by 65 µL of 10 % (w/v) CTAB (cetyltrimethylammoniumbromid). After an incubation of 30 min at 65 °C, 700 µL of (24:1) chloroform/isoamylalcohol was added, the tubes were mixed carefully by hand, stored on icy water for 30 min, and centrifuged for 10 min at 4 °C (10 000 g). The supernatant was recovered and the genomic DNA precipitated using isopropanol. After washing the pellets with 70 % ethanol, they were dried in a vacuum centrifuge and re-suspended in 60 µL of TE buffer (protocol modified from Möller et al. 1992).

Six regions covering five genes were amplified: nucLSU, nucSSU, mtSSU, RPB1 region A–D, RPB2 region 5–7, and RPB2 region 7–11 (see Table 2 for primers used). Genomic DNA (1 µL of a 1:10 or 1:100 dilution) was added to a PCR mix comprising 2.5 µL of PCR buffer (buffer IV with 15 mM MgCl₂, Abgene, Epsom, U.K.), 2.5 µL of dNTPs (2 mM), 2.5 µL of BSA (10 mg/mL), 2.0 µL of primers (10 µM), 0.15 µL Taq polymerase (5 U/µL, Denville, Metuchen, NJ, U.S.A.), and water for a total volume of 25 µL. Amplification cycles for nucLSU, nucSSU and RPB1 (same conditions applied for RPB2) are described in Gueidan et al. (2007), and in Zoller et al. (1999) for mtSSU. The PCR products were purified using Microcon PCR cleaning kits (Millipore, Billerica MA, U.S.A.). Sequencing was carried out using Big Dye Terminator Cycle sequencing Kits (ABI PRISM version 3.1, Perkin-Elmer, Applied Biosystems) on ABI 3730xl DNA Analyzers (Applied Biosystems, Foster City CA, U.S.A.) from the Duke Center for Evolutionary Genomics (Durham NC, U.S.A.) and the Hubrecht Institute (Utrecht, Netherlands).

Table 2. List of primers for the five genes used in this study (RPB2 was amplified in two regions).

<table>
<thead>
<tr>
<th>Gene regions</th>
<th>PCR primers</th>
<th>Additional primers used for sequencing</th>
</tr>
</thead>
<tbody>
<tr>
<td>nucLSU</td>
<td>LR0R, LR7</td>
<td>LR3, LR3R, LR5, LR5R, LR6, LR6R</td>
</tr>
<tr>
<td>mtSSU</td>
<td>mtSSU1, mtSSU3R</td>
<td>mtSSU2, mtSSU2R8</td>
</tr>
<tr>
<td>RPB1 region A–D</td>
<td>RPB1-4F, RPB1-6R1asc</td>
<td>–</td>
</tr>
<tr>
<td>RPB2 region 5–7</td>
<td>RPB2-5F, RPB2-7cR</td>
<td>–</td>
</tr>
<tr>
<td>RPB2 region 7–11</td>
<td>RPB2-7cF, RPB2-11aR</td>
<td>–</td>
</tr>
</tbody>
</table>

Alignments and phylogenetic analyses

Sequences were assembled and edited using Sequencher (Genes Codes Corporation, Ann Arbor MI, U.S.A.). Manual alignments were performed using MacClade v. 4.08 (Maddison & Maddison 2003). Ambiguous regions (sensu Lutzoni et al. 2000) and introns were delimited manually and excluded from the alignments. Congruence was tested using a 70 % reciprocal bootstrap criterion (Mason-Gamer & Kellogg 1996, Reeb et al. 2004). For the three-gene dataset, the test was performed using Compstat (Kauf & Lutzoni 2002) on all possible gene pairs (mtSSU vs. nucSSU, mtSSU vs. nuclSU, and nuclSU vs. nucSSU) and based on bootstrap consensus trees. Bootstrap trees were obtained using Neighbor-Joining bootstrap analyses with Maximum Likelihood distances in PAUP v. 4.0b10 (Swofford 2003). Models of molecular evolution were estimated using the Akaike Information Criterion implemented in Modeltest v. 3.7 (Posada & Crandall 1998). For the five-gene dataset, congruence was also tested using a 70 % reciprocal bootstrap criterion, but the comparison was done manually based on trees obtained with 500 bootstrap replicates using RAxML VI-HPC (Stamatakis et al. 2005, 2008) on the Cipres Web Portal (www.phylo.org/sub_sections/portal/). Taxa or sequences responsible for incongruence were removed from the dataset, and the markers were combined. Final phylogenetic analyses of the three-gene and five-gene datasets were performed using RAxML on the Cipres Web Portal. The ML search followed a GTRMIX model of molecular evolution applied to the following nine partitions: RPB1 first, second and third codon positions, RPB2 first, second and third codon positions, nuclLSU, nucSSU and mtSSU. Support values were obtained with bootstrap analyses of 1 000 pseudoreplicates using RAxML.

RESULTS

DNA sequence alignments

Not all markers were recovered or available for all taxa. For the three-gene dataset, 20 nuclLSU, 11 nucSSU and 54 mtSSU sequences were missing. Among the 182 taxa, 119 had sequences for three genes, 61 for two genes, and 12 for one gene (Table 1 in Supplementary Information). After exclusion of ambiguous regions and introns, the combined dataset included 3 274 characters (1 106 for nuclLSU, 1 616 for nucSSU and 552 for mtSSU). Among these, 2 063 were constant while 931 were parsimony-informative. For the five-gene dataset, missing data comprised 5 nuclLSU, 8 nucSSU, 30 mtSSU, 48 RPB1 and 30 RPB2 sequences. Among the 113 taxa, 32 had sequences for five genes, 46 for four genes, 30 for 3 genes, and 5 for 2 genes (Table 1 in Supplementary Information). After exclusion of ambiguous regions and introns, the combined dataset included 6 045 characters (1 133 for nuclLSU, 1 607 for nucSSU, 593 for mtSSU, 1 011 for RPB1 and 1 701 for RPB2). Among these, 2 912 were constant while 2 693 were parsimony-informative.

Phylogenetic inference

For the three-gene analysis (Figs 2–3), results show that, within the two classes Dothideomycetes and Arthroniomycetes, rock-inhabiting fungi belong to 13 groups, either well-known orders or families, or lineages that have not previously been characterised. Among the rock-inhabiting fungi clustering with well-known groups of Dothideomycetes, two strains are found in the order Dothideales, four in the order Pleosporales, one in Myriangiales, 12 forming a monophyletic group sister to the remaining members of Davidiellaceae, and one in the family Capnodiaceae. The family Teratosphaeriaceae is not monophyletic in this analysis (also see Crous et al. 2009). In a first group including the generic type Teratosphaeria fibrillosa (Teratosphaeriaceae 1, Fig. 3), many rock-inhabiting strains are present, including taxa from the three genera Friedmanniomyces, Elastomycyes and Recurvomyces. The second group (Teratosphaeriaceae 2, Fig. 3), including the three leaf-colonising species Devriesia streitziaceae, Mycosphaerella eurypotami and Tripospermum myrti, an unknown species of Capnodiaceae, the lichen species Cystococcus ebenus as well as 20 undescribed rock inhabiting strains, is supported as sister to the family Mycosphaerellaceae (91 % bootstrap). The two rock-inhabiting species Coniosporium uncinatum and C. apollinis are well supported (100 % bootstrap), but their sister relationship is not. Neither these two species of Coniosporium nor the Antarctic genus Cryomyces can be assigned to any known family or order sampled here. Amongst the unknown lineages, one does not seem to be part of Dothideomycetes (lineage 1, Fig. 2), and appears as sister to Arthroniomycetes (98 % bootstrap). Due to the lack of support for many deep internodes, it is not possible to determine if lineages 2 and 3 can be accommodated by the expansion of known groups of Dothideomycetes, or if the recognition of new taxonomical entities are needed. Finally, the rock isolates A6, AN13, TRN 437 and CCFE 5413 do not significantly cluster with any other taxa.

With the five-gene analysis (Fig. 4), the inferred deep branching pattern within Dothideomyceta is still poorly supported, but additional well-supported nodes are recovered (e.g., Capnodiaceae as sister to the lineage including Mycosphaerellaceae and Teratosphaeriaceae, and the monophyly of Teratosphaeriaceae 1). As in the three-gene analysis, the sister relationship between lineage 1 and Arthroniomycetes obtains high support (100 % bootstrap), even though the two rock-inhabiting strains included do not seem to form a monophyletic group. The placement of the lichen family Trypetheliaceae as sister to Arthroniomycetes (70 % bootstrap) might be an artifact, as this relationship was not recovered in any other studies (Del Prado et al. 2006, Spatafora et al. 2006, Nelsen et al. 2009). Within Dothideomycetes, the orders Dothideales and Myriangiales form a sister group (100 % bootstrap), and are sister to the well-supported Capnodiaceae (100 % bootstrap), which includes most of the rock-inhabiting strains. Within Capnodiaceae, the second group of Teratosphaeriaceae (Teratosphaeriaceae 2, Fig. 4) is still supported as sister to Mycosphaerellaceae (89 % bootstrap). Other lineages comprising exclusively RIF (Cryomyces, Coniosporium uncinatum, and C. apollinis) do not significantly cluster with any known group of Dothideomycetes.
Fig. 2. Phylogenetic placement of 102 rock-inhabiting strains within Dothideomycetes (Dothideomycetes and Arthoniomycetes). The tree is based on a Maximum Likelihood analysis of the combined nuLSU, nucSSU and mtSSU (three-gene analysis). A black oval on a branch indicates a bootstrap support value of 100 %. Other bootstrap values ≥ 50 % are shown below or above branches. RIF are highlighted in red and lichens in green. Geographical origins are also labeled for RIF (Alp = Alps, And = Andes, Ant = Antarctica, Ari = Arizona desert, Cri = Crimea, Fra = France, Med = Mediterranean region, including Greece, Israel, Italy, Slovenia, Spain and Turkey). Phylogenetic relationships within Capnodiales are detailed in Fig. 3.
Fig. 3. Phylogenetic placement of RIF within the order Capnodiales. The tree is based on a Maximum Likelihood analysis of the combined nucLSU, nucSSU and mtSSU (three-gene analysis). A black oval on a branch indicates a bootstrap support value of 100 %. Other bootstrap values ≥ 50 % are shown below or above branches. RIF are highlighted in red and lichens in green. Geographical origins are also labeled for RIF (Alp = Alps, And = Andes, Ant = Antarctica, Ari = Arizona desert, Cri = Crimea, Fra = France, Med = Mediterranean region, including Greece, Israel, Italy, Slovenia, Spain and Turkey).
Fig. 4. Phylogenetic relationships of rock-inhabiting lineages with known groups of Dothideomycetes based on a Maximum Likelihood analysis of the combined nucLSU, nucSSU, mtSSU, RPB1 and RPB2 (five-gene analysis). A black dot on a branch indicates a bootstrap support value of 100%. Other bootstrap values ≥ 50% are shown below or above the branches. RIF are highlighted in red and lichens in green.
DISCUSSION

Species diversity in Dothideomycetes

The Dothideomycetes are very diverse in terms of species, some of which are well known for their pathogenicity on crops (e.g., Mycosphaerella fijiensis, the agent of the leaf spot disease of banana, or Leptosphaeria maculans, the agent of the blackleg disease of cabbage). Whilst many species are associated with plants (either as pathogens or as epiphytes), saprobic, coprophilous, lichen-forming and rock-inhabiting fungi are also present in this class. The importance of RIF in terms of species richness is still under-investigated. A thorough sampling of dothideomycetous RIF from few localities in Mallorca and Central Spain formed the basis of the analyses described here (Ruibal et al. 2005, 2008). RIF from the Alps and the Andes (Selbmann et al. 2005, 2008), as well as the Arizona and Negev deserts (Staley et al. 1982, A.A. Gorbushina, unpubl. data) extended the geographical range of the sampled taxa. Finally, isolates from monuments in the Mediterranean area supplemented the sampling (Gorbushina et al. 1996, Sterflinger et al. 1997, Volkman & Gorbushina 2006). In comparison to known RIF habitats (Gorbushina 2007), our sampling was very restricted and does not permit a realistic overview of fungal diversity on rock surfaces. Nevertheless, an impressive number of rock-inhabiting species is already evident. Our data show that rock-inhabiting fungi are not only present in well-known orders, such as Capnodiales or Pleosporales, but also in novel lineages (e.g., lineage 1, Fig. 2). Moreover, very few species with overlapping distribution were recovered from neighbouring geographical localities in Mallorca and Central Spain (Ruibal et al. 2005, 2008). Therefore, we can hypothesise that species richness within Dothideomycetes remains woefully underestimated, and that many more species will need to be described within this class in the future, especially for fungi colonising rocky substrates.

Classification of rock fungi related to Dothideomycetes

Although very diverse within Dothideomycetes, RIF have not been included in recent phylogenetic studies of this class (Lumbsch et al. 2001, Schoch et al. 2006). Only very few of these rock-inhabiting species have been taxonomically described (Sterflinger et al. 1997, Bills et al. 2005, Sert et al. 2007b), and the molecular marker available for most of these species (ITS) does not allow their inclusion in large-scale phylogenetic analyses. The few attempts to produce phylogenies involving RIF have shown that they belong to two diverse classes of Ascomycota, namely Eurotiomycetes (particularly the order Chaetothyriales) and Dothideomycetes (preponderantly the orders Capnodiales, Dothideales and Pleosporales) (Sterflinger et al. 1999, Ruibal 2004, Ruibal et al. 2005, 2008).

Our results confirm the placement of RIF in the same orders of Dothideomycetes, although some lineages are shown to belong to additional groups. Based on our results, many RIF should be classified within Dothideales, Pleosporales and Capnodiales, the latter order holding the largest number in rock-colonising species. The genera Elasticomyces and Recurvomyces, as well as the Antarctic genus Friedmanniomyces, were previously attributed to Capnodiales based on nucSSU data (Selbmann et al. 2008). Our multigene analyses confirm this placement, and show that these three genera belong to Teratosphaeriaceae s. str., the family currently showing the highest diversity in RIF (Fig. 3). We also showed that one RIF (TRN 235) previously thought to be related to Dothideales (Ruibal et al. 2008) actually belongs to Myriangiales, along with Sarcinomyces crustaceus, a species similarly melanised and meristematic, but isolated from plant material (Sigler et al. 1981).

Several well-supported groups of RIF could not be attributed to any known families and orders according to our data. As a consequence, Cryomyces should still be considered as Dothideomycetes incertae sedis, as no close relationship was recovered for this enigmatic Antarctic genus (Selbmann et al. 2005). The positions of RIF-rich genera Coniosporium and Sarcinomyces are also problematic. Previous studies placed them either in Dothideales or Chaetothyriales based on ITS or nucSSU data (de Leo et al. 1999, Sterflinger et al. 1999, Sert et al. 2007a). Yet, the limited taxon and gene sampling on which these analyses were based was probably insufficient to demonstrate clear phylogenetic relationships. Our results show that Coniosporium apollinis (including the type strain CBS 352.97), C. uncinatum (including the type strain CBS 100219) and Sarcinomyces crustaceus belong to Dothideomyceta (Fig. 4). However, a previous multigene analysis showed that two other species, Coniosporium perforans and Sarcinomyces petricola, belong to Chaetothyriales (Gueidan et al. 2008). These anamorphic genera are therefore not monophyletic, and additional research is required to clarify their status.

Among lineages lacking known reference taxa, two groups seem to belong to Dothideomycetes (unknown group 2, a lineage comprising RIF from the Alps, and unknown group 3, a lineage including strains isolated in Arizona; Fig. 2). Another unknown group (lineage 1) clusters outside Dothideomycetes, sister to the Arthoniales (Figs 2, 4). A previous study had noted the problematic placement of this latter group (Ruibal et al. 2008). Many lineages including RIF still need to be named. In the past, several melanised meristematic species and genera have been described such as Lichenothelia (Hawksworth 1981; see also Henssen 1987), which could potentially correspond to some of these RIF lineages. However, little is known about these formerly named taxa, and no molecular data or cultures are available for many of them. Naming RIF will therefore require an extensive study of both rock-inhabiting species and formerly described melanised meristematic species, whether they grow on rock or not.

Rock surfaces: “terroirs” for ancient lineages or reservoirs for plant-associated fungi?

Despite the prevailing extreme conditions, rock surfaces host a large variety of specialised fungi. Fungal colonisation of subaerial rocks can be explained by two non-exclusive hypotheses. Firstly, atmosphere-exposed rock substrates could constitute “terroirs” for ancient fungal lineages. Rock surfaces were among the first terrestrial substrates available for living organisms on earth (Gorbushina & Broughton 2009). It is therefore likely that, early on, some species became adapted to colonise rock surfaces. RIF are persistent to different types of physical stress, but are poor competitors and surrender to more combative organisms (Gorbushina et al. 2008). Increasing competition with other rock-inhabiting organisms living under more permissive conditions may have restricted some of these ancient, morphologically reduced, slow-growing, fungal relicts to extreme habitats. The presence of lineages comprising exclusively RIF that diverged early in the evolution of Dothideomyceta (e.g., Cryomyces and lineage 1, Fig. 2) supports this hypothesis of rock surfaces as substrates for ancient fungal lineages.
Secondly, rock surfaces could form reservoirs for plant-associated or saprobic fungi. Through spore or propagule dispersal, some species of various unrelated groups of plant pathogens, epiphytes or saprobes can reach rock substrates. Their ability to survive in these environments will depend on some key features, namely oolytropy, melanisation and pleiomorphism (or diversity of growth forms, amongst which meristematic growth). Under extreme conditions prevailing on rock surfaces, fungi possessing these key features can survive due to their slow, meristematic, clumpy growth and thick-walled, heavily melanised cells. These key features seem to have evolved several times in and thick-walled, heavily melanised cells. These key features seem to have evolved several times in

**Phylogeny of rock-inhabiting fungi related to Dothideomycetes**

Most of the diversity in lichen-forming fungi is found in Lecanoromycetes, a large and diverse class of ascomycetes including approximately 14 000 species (Müller-Dobler et al. 2006). Yet, the classes Lichinomycetes (with the single order Lichinales), Eurotiomycetes (with the orders Pyrenulales and Verrucariales), Arthoniomycetes (with the single order Arthoniales), and Dothideomycetes also include lichens. Although Lichinales, Pyrenulales, Verrucariales and Arthoniales are monophyletic lineages containing mostly lichenised species, lichens in Dothideomycetes seem to encompass a broader phylogenetic spectrum: the Trachypeltidaeae, a family of mostly tropical bark-colonising lichens, forms a monophyletic group within Dothideomycetes (Del Prado et al. 2006, Selbmann et al. 2009). Athyrioprenia salicis, a corticolous, temperate lichen species nests within the order Pleosporales (Del Prado et al. 2006, Selbmann et al. 2009). Two melanised micro-flamentous lichens, Cystoleucus ebeens and Racodium rupestre, were assigned to the order Capnodiates (Muggia et al. 2008, Selbmann et al. 2009). Finally, the two lichen families Strigulaceae (mostly leaf-colonising tropical species) and Monoblastaceae (temperate and tropical species) are now shown to belong to Dothideomycetes (Selbmann et al. 2009; this volume).

Whether these lichen lineages, that are unrelated to Lecanoromycetes, originated from independent gains of lichenisation is not clear (Lutzoni et al. 2001, James et al. 2006, Gueidan et al. 2008, Arnold et al. 2009, Schoch et al. 2009a, b). Within Eurotiomycetes, phylogenetic data suggest that the lineage including Pyrenulales and Verrucariales possibly results from an independent gain of lichenisation (Gueidan et al. 2008, Schoch et al. 2009a, b). Phylogenetic data suggest that lichens in Verrucariales may have evolved from rock-inhabiting fungi (Gueidan et al. 2008), a result in agreement with experimental data demonstrating that some RIF and one melanised lichen-colonising fungus could form associations with lichen-associated algae (Gorbushina et al. 2005, Brunauer et al. 2007). This rock-inhabiting ancestor may have evolved associations with epithlial microalgae in order to get a more constant supply in nutrients. If the evolution of fungal-algal associations occurred in Eurotiomycetes, it most likely also occurred in different fungal groups. It is therefore interesting to see if in Dothideomycetes, where rock fungi are so diverse, similar transitions in lifestyles can be suggested.

Although many lichenised species in Dothideomycetes are either corticolous or only secondarily or occasionally saxicolous, Cystoleucus ebeens and Racodium rupestre are true rock inhabitants. Amongst lichens in Dothideomycetes, these two species are the most likely to have evolved from a rock-inhabiting ancestor. They share substrate preference and some morphological features, such as their melanised hyphae, with RIF. Strikingly, in our result, Cystoleucus ebeens is nested within a lineage comprising almost exclusively RIF (Teratosphaeriaceae 2, Fig. 3).
Racodium rupestre is also related to a Rif, but this relationship is not supported (Fig. 3). This result agrees with a rock-inhabiting ancestor for these two lichenised species, but further data will however be necessary to test this hypothesis. Also of interest is the close phylogenetic relationship between the lichen order Arthoniales and the lineage 1 of Rif (Figs 2, 4). Although mostly corticolous or foliicolous, Arthoniales also comprises saxicolous species (Ertz et al. 2009). Further data is needed to explore the relationships between saxicolous species of Arthoniales and Rif. In conclusion, these preliminary results suggest that there might be a link between rock-dwelling habit and lichenisation. However, additional taxon and gene sampling are needed to confirm the phylogenetic placements of some of the lichenised taxa and to clarify their relationships to Rif. Only then the hypothesis of Rif as ancestors of lichenised lineages can be adequately tested.

ACKNOWLEDGEMENTS

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REFERENCES


Table 1. Taxon and gene sampling for the three- and five-gene analyses. Geographical origins are also mentioned for RIF. A dash indicates missing sequences. Newly produced sequences are shown in bold. A column also indicates if taxa were included in the three-gene (3) or in both three- and five-gene analyses (3 & 5).

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