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 tolerate 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 Teratospoerales z.l.), Dothideales, Pleosporales, and Mnyriangiaceae, 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 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