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The sterile microfilamentous lichenized fungi *Cystocoleus ebeneus* and *Racodium rupestre* are relatives of plant pathogens and clinically important dothidealean fungi

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ABSTRACT

The phylogenetic positions of the always-sterile microfilamentous lichens *Cystocoleus ebeneus* and *Racodium rupestre* were studied in a phylogenetic framework using sequence data of 5' nuSSU, nuLSU, and mtSSU rDNA. The analysis reveals that both genera are ascomycetes and belong to Dothideomycetidae: they are not close to lichenized members within the subclass, but rather belong to Capnodiales. The macroscopically scarcely distinguishable *C. ebeneus* and *R. rupestre* do not form a monophyletic group. The well-supported clade of *R. rupestre* is basal to the one in which *C. ebeneus* is close to *Mycosphaerellaceae*. This study provides another example of ascomycetes with very different life-styles and ecologies being closely related.

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Introduction

The phylogenetic relationships of various sterile, lichen-forming fungi are gradually being resolved by molecular phylogenetic methods. The majority of studies carried out so far with sterile lichens confirmed placements close to particular lichenized species as suggested by similarities in thallus shapes or secondary chemistry. These alone were misleading in earlier classifications of morphologically distinct species:

'*Lecanora demissa*' proved to be an anthraquinone-devoid member of *Caloplaca* (Arup & Grube 1999), and '*Lecanora lisboensis*' proved to merit recognition as an independent genus *Coscinocladium* in *Physciaceae* (Crespo *et al.* 2004). Studies on previously unclassified sterile lichen genera have also revealed that similarities in thallus structures are not necessarily indicative of monophyletic relationships. Ekman & Tønsberg (2002) discovered that the majority of the strictly sterile and sorediate *Lepraria* species form a monophyletic

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lineage related to *Stereocaulaceae*, but one of the species was related to *Lecanoraceae* (i.e. *Lecanora rouxii*) (Grube *et al.* 2004), and another apparently belongs to *Verrucariaceae* (i.e. *Botryolepraria lesdainii*) (Grube, unpubl.). The asexual erect shrubby genus *Siphula* (*Icmadophilaceae*) (Stenroos & DePriest 1998) represents a similar case. Although always regarded as a clearly natural genus of sterile species, molecular studies indicate that *Siphula* is not monophyletic (Stenroos *et al.* 2002; Grube & Kantvilas 2006). In addition to these ‘well-formed’ sterile lichens with a rather conventional layered or sorediate thallus organization, there are other fungal–algal associations that might not be so closely related to the main lichenized lineages.

Cystocoleus ebeneus and *Racodium rupestre* are geographically widespread lichens with a peculiar microfilamentous growth. Both form associations with *Trentepohlia* algae, in which the filamentous photobionts are firmly enclosed as a central axis by melanized fungal hyphae. The enveloping mycelium comprises only a single cell layer: in *C. ebeneus* the hyphae are irregularly wrinkled and somewhat twisted around the algal filament, whereas in *R. rupestre* they are arranged parallel to the axis with elongate rectangular cells. In these two genera, the fungal partner is the exhabitant (following the definition of Hawksworth & Honegger 1994), but in contrast to most other lichens, the alga dictates the thallus morphology, whereas the fungus only plays a minor role in shaping the microfilamentous thallus, but is responsible for the dark colour of the filaments. This type of thallus is seen also in few other lichen lineages, notably in *Coenogonium* (*Gyalectaceae*, associating with *Trentepohliaceae*) (Uyenco 1963), *Ephebe* (*Ephebeaceae*, with *Stigonema*) (Henssen 1963), and *Pyrenothrix* (with *Scytonema*) (Eriksson 1981; Herrera-Campos *et al.* 2005). The associations are also similar to microfilamentous species of the mainly tropical lichenized basidiomycete genus *Dictyonema*.

Both *Cystocoleus ebeneus* and *Racodium rupestre* frequently occur together on the same rocks, and are almost indistinguishable without a microscope, to the extent that we wondered whether their separation by the arrangement of the enveloping hyphae of the *Trentepohlia* filaments was justified. Both genera form small to medium-size felt-like patches that may coalesce to give an extensive carpet-like cover, and both occur in shaded and cool-humid habitats of under hanging or vertical siliceous rocks that do not receive direct rainfall.

C. ebeneus appears to have a wider ecological amplitude than *R. rupestre*, and is also known from soil and eroded moss cushions in the subantarctic islands (Jørgensen 1986).

The position of *C. ebeneus* and *R. rupestre* within the *Ascomycota* was completely unknown due to the lack of diagnostic sexual or asexual structures or any characteristic lichen products, and the genera were omitted from a recent synopsis of ascomycete genera (Eriksson 2006). Moreover, the nomenclature of both monotypic genera is complex and requires new lectotypifications; this information and also data on the world distribution and morphology of these and a new tropical genus mentioned with some shared characteristics being finalized for presentation separately (Rolf Santesson & Hawksworth, unpubl.). In this study we investigate the phylogenetic position and independence of these enigmatic lichens using several ribosomal gene loci, which show they are within *Dothideomycetes*.

Materials and methods

Sampling

Sixteen thalli of *Cystocoleus ebeneus* and three of *Racodium rupestre* were collected in six localities in Austria, and two further thalli of *R. rupestre* were collected in Italy and in the UK (Table 1). All voucher material is stored in the collections of the Institute of Plant Sciences, Graz (GZU) and the University of Trieste (TSB).

Some thalli of *R. rupestre* were found in small patches growing almost intermixed with the thalli of *C. ebeneus*. For this reason we carefully checked all individual thallus patches under the dissecting microscope (Leica M3Z, Vienna) to select homogeneous material that was free of any other fungal organisms (including the very frequent presence of *Lepraria* soredia).

Molecular analysis: DNA isolation, PCR amplification, and sequencing

In clean lichen material the identity of either *Cystocoleus ebeneus* or *Racodium rupestre* was checked using an optical microscope (Zeiss Axioskop, Vienna). DNA was isolated according to Cubero *et al.* (1999). For some thalli more than one DNA extraction was performed to confirm the results.

Table 1 – Geographic provenience of the samples

Locality	<i>Cystocoleus ebeneus</i>	<i>Racodium rupestre</i>
Austria, Styria, Koflach, Edelschrott, Jurikogel, 2005, Hafellner & Muggia (GZU).	× (L161)	
Austria, Styria, Seckauer Tauern, Zinkenbachgraben, 2006, Hafellner & Muggia (GZU).	× (L315)	
Austria, Carintia, Sterisches Randgebirge, Stubalpe, Höllgraben, 2006, Hafellner & Muggia (GZU).	×	
Austria, Styria, Koralpe, Deutschlandsberg, Laßnitz Klause, 2006, Hafellner & Muggia (GZU).		×
Austria, Styria, Koralpe, Reinischkogel-Massiv, Judanderl, 2006, Hafellner & Muggia (GZU).	×	×
Austria, Styria, Koralpe, Reinischkogel-Massiv, Straußkogel, 2006, Hafellner & Muggia (GZU).	× (L348)	× (L346)
Austria, Carintia, Stubalpe, Lichtengraben, Goldbründl, 2006, Hafellner & Muggia (GZU).	× (L364)	
Italy, Trentino Alto Adige, Mt. Stelvio National Park, 2006, Muggia & Hafellner (TSB).		× (L424)
United Kingdom, North Devon, Dartmoor National Park, 2006, Hawksworth (GZU).		× (L423)

Samples selected for the phylogenetic analysis are mentioned in parenthesis with their isolation numbers (DNA isolation are represented by ×).

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