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Evolutionary relationships among aquatic anamorphs and teleomorphs: *Lemonniera*, *Margaritispora*, and *Goniopila*[☆]

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ABSTRACT

The hypothesis that similar conidial morphologies in aquatic hyphomycetes are a result of convergent evolution was tested using molecular sequence data. Cladistic analyses were performed on partial sequences of 28S rDNA of seven species of *Lemonniera*, one species of *Margaritispora* and one species of *Goniopila*. *Lemonniera* has tetra- or polyradiate conidia with long arms, whereas *Margaritispora* and *Goniopila* have typically globose (isodiametric) conidia, with short conical protuberances in a stellate or quadrangular arrangement. *Lemonniera* and *Margaritispora* have phialidic conidiogenesis and both produce dark, minute sclerotia in culture whereas *Goniopila* has holoblastic conidiogenesis and does not produce sclerotia in culture. *Goniopila* produces a microconidial phialidic synanamorph in culture. All three genera have schizolytic conidial secession. Molecular analyses demonstrate that *Lemonniera* species are placed in two distinct clades: one within *Leotiomycetes*; the other within *Pleosporales*, *Dothideomycetes*. *Margaritispora* is placed with *Lemonniera* species within *Leotiomycetes*. *Goniopila* and *Lemonniera pseudofloscula* are placed within *Dothideomycetes*. No morphological character was entirely congruent with the molecular derived phylogeny. This suggests that for the group of species studied, conidial shape is not a reliable indicator of phylogeny but more likely the result of convergent evolution in response to the aquatic environment.

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Introduction

An ascomycete species may exist as a pleomorphic holomorph, a teleomorph, or an anamorph (Reynolds 1993; 1994). Teleomorphs and pleomorphic holomorphs are classified based primarily on the morphology of sexual reproductive structures, whereas anamorphs have traditionally been classified based on their method of conidiogenesis, conidium and conidiophore morphology, and conidial secession. It

was once thought that eventually sexual states would be identified for most anamorphs, thereby obviating the need of a separate classification system for anamorphic states. However, relatively few connections have been made (Kendrick 1991) and connections have not always been predictive (Kendrick & Murase 1994). Current evidence suggests that anamorphs are probably derived from pleomorphic holomorphs through loss of the ability to morphologically express sexual reproduction (de Bary hypothesis) (Reynolds 1994). This suggests that

[☆] Dedicated to John Webster on the occasion of his 80th birthday.

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anamorphs will always exist and that identifying their teleomorphic states through cultural studies (Kendrick 1979; Reynolds 1994) is unlikely to be successful for most taxa. Recently, mycologists have turned to molecular sequence data as a source of information on the phylogenetic relationships of anamorphic fungi (Berbee & Taylor 1993; O'Donnell 1993; Platt & Spatafora 2000).

The aquatic ('Ingoldian') hyphomycetes are well-known for their morphologically distinctive conidial shapes: sigmoid, tetra- or polyradiate, or variously branched. These conidial morphs are considered to be adaptive to the aquatic habitat and facilitate attachment and/or dispersal in flowing water (Webster 1959). Ingold (1975) speculated that convergent evolution has probably occurred in this group resulting in a somewhat artificial classification. He based this idea on the observation that taxa with tetra- or polyradiate conidia have different types of conidiogenesis. Recently, freshwater species of *Anguillospora*, a genus characterized by sigmoid conidia and holoblastic conidiogenesis, has been linked culturally to six genera representing three different classes of Ascomycota (Shearer <http://fm5web.life.uiuc.edu:23523/ascomycete/>). This lends further support to the idea of convergent evolution in conidial morphology in aquatic hyphomycetes.

Our aim in this study was to use molecular data to further test the idea of convergent evolution put forth by Ingold (1975). We also wanted to determine where these anamorphic aquatic fungi would be placed in the pleomorphic phylogenetic system using molecular data. We selected three aquatic hyphomycete genera that have no known teleomorph connections. *Lemonnieria* is characterized by tetra- or polyradiate conidia with long arms, phialidic conidiogenesis, and the formation of minute dark sclerotia in culture; seven species are recognized: *L. alabamensis*, *L. aquatica* (type of the genus), *L. centrosphaera*, *L. cornuta*, *L. filiformis*, *L. pseudofloscula*, and *L. terrestris* Tubaki. *Margaritispora* is also characterized by phialidic conidiogenesis, and by the production of minute dark sclerotia in agar culture. However, the conidia are typically dimorphic: when formed under water they are globose or tetrahedral with short, papilliform or conoid protuberances; when formed at the water-air interface they are mostly fusiform; the genus is monotypic, based on *M. aquatica* (*M. hongkongensis* mentioned in Ho et al. 2002 is a *nomen nudum*; Kevin D. Hyde, pers. comm.). *M. monticola* was placed in the new genus *Goniopila* (Marvanová & Descals 1985). *G. monticola* is monotypic and has globose conidia with short conoid protuberances; the

detached conidia are difficult to differentiate from those of *M. aquatica*. However, unlike *Lemonnieria* or *Margaritispora*, *Goniopila* produces conidia holoblastically, does not produce dark sclerotia in culture, and has a microconidial phialidic synanamorph. All three genera have schizolytic conidial secession.

Materials and methods

Collection, isolation and characterisation

Cultures of the species used in this study were obtained from collections made from streams in Europe and Canada (Table 1) and are maintained in the Czech Collection of Microorganisms (CCM). Permanent specimens made from sporulating cultures are also deposited in CCM. Isolation was always mono-conidial except for *Lemonnieria cornuta*, where this information is lacking. A loop full of fresh foam was streaked onto a microscope slide coated with a thin layer of malt extract agar (MEA; 0.1–2% plus 100 mg l⁻¹ chloramphenicol or penicillin/streptomycin) and kept at 10–15 °C. After 24–48 h, germinating conidia were transferred to 2% MEA plates and stored at 10–18 °C (Marvanová & Bärlocher 1998; Marvanová & Gulis 2000). Before processing, cultures were checked for bacterial and fungal contaminants, subcultured to potato dextrose agar (PDA) plates and incubated at 15 °C for 6–8 wk.

DNA extraction, sequencing and phylogenetic analysis

DNA was extracted, amplified and sequenced following the procedures of Campbell et al. (2003). Additional sequences were obtained from GenBank (Table 2). Representatives from 17 orders of ascomycetes, and four species of basidiomycetes as outgroup taxa, totalling 291 taxa, were included in our analyses. Initial analyses were performed in PAUP 4.0b10 (Swofford 2002) using MP criteria with heuristic searches employing simple sequence addition using *Agaricus arvensis* as a reference taxon. Gaps were treated as missing data and a tree bisection-reconnection branch-swapping algorithm was used.

For the second data set, species that were not closely related to the selected aquatic hyphomycetes were removed. Inclusion and exclusion of taxa was based upon the results

Table 1 – Fungal isolates used in this study

Species	Culture no.	Isolated by	Country of origin	GenBank accession no.
<i>Lemonnieria aquatica</i>	CCM F-21799	L. Marvanová	Czech Republic	DQ267627
<i>L. centrosphaera</i>	CCM F-21094	L. Marvanová	Canada	DQ267628
<i>L. cornuta</i>	CCM F-325	J. Webster	UK	DQ267629
<i>L. filiformis</i>	CCM F-19599	L. Marvanová	Austria	DQ267630
<i>L. pseudofloscula</i>	CCM F-0484	L. Marvanová	Czech Republic	DQ267631
<i>L. pseudofloscula</i>	CCM F-43294	L. Marvanová	Canada	DQ267632
<i>L. terrestris</i>	CCM F-11486	L. Marvanová	Slovak Republic	DQ267634
<i>Lemonnieria</i> sp.	CCM F-19299	L. Marvanová	Czech Republic	DQ267633
<i>Margaritispora aquatica</i>	CCM F-11591	L. Marvanová	Czech Republic	DQ267635
<i>Goniopila monticola</i>	CCM F-11686	L. Marvanová	Slovak Republic	DQ267626

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