

Testing morphology-based hypotheses of phylogenetic relationships in Parmeliaceae (Ascomycota) using three ribosomal markers and the nuclear *RPB1* gene

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Abstract

Parmeliaceae is the largest family of lichen-forming fungi with more than 2000 species and includes taxa with different growth forms. Morphology was widely employed to distinguish groups within this large, cosmopolitan family. In this study we test these morphology-based groupings using DNA sequence data from three nuclear and one mitochondrial marker from 120 taxa that include 59 genera and represent the morphological and chemical diversity in this lineage. Parmeliaceae is strongly supported as monophyletic and six well-supported main clades can be distinguished within the family. The relationships among them remain unresolved. The clades largely agree with the morphology-based groupings and only the placement of four of the genera studied is rejected by molecular data, while four other genera belong to clades previously unrecognised. The classification of these previously misplaced genera, however, has already been questioned by some authors based on morphological evidence. These results support morphological characters as important for the identification of monophyletic clades within Parmeliaceae.

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1. Introduction

Symbiotic associations with photosynthetic active partners, such as algae or cyanobacteria, are among the most widespread life strategies of fungi and are especially common in Ascomycota. Roughly 40% of all Ascomycota form such symbiotic relationships that are called lichens (Kirk

et al., 2001). Unlike most non-lichenized fungi, lichens have a diverse vegetative morphology as a consequence of their dual nature. These morphologies primarily reflect the necessity of these symbiotic systems to expose sufficient area with algae or cyanobacteria to light for photosynthesis. Foliose lichens for example have a leaf-like appearance while fruticose lichens increase their surface by dividing the thalli to form branches (Ott and Lumbsch, 2001). The water regime plays another important role in the morphology of lichens. In foliose lichens a water film between the thallus and the contacting substrate can be gradually taken up by

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the lower surface (Jahns, 1984). Since water uptake occurs over the whole surface of the lichen thallus, deeply divided fruticose lichens have been shown to be extremely effective in use of fog, snow or dew (e.g., Lange et al., 1990); epicortical thin polysaccharide layers interrupted by several structures as pores, fenestrations (Blanco et al., 2004a) or pseudocyphellae also play an important role in water isolation and gas exchange (Hale, 1973). The different morphologies found in lichens have been widely used in taxonomy of these organisms. However, molecular studies demonstrated that growth forms are of no importance at the family and in some cases even generic level (e.g., Stenroos and DePriest, 1998; Wedin et al., 1999; Ekman, 2001; Schmitt et al., 2001; Blanco et al., 2004b). While these phylogenetic studies showed that morphology cannot be schematically applied to circumscribe higher taxa, there is no random pattern of morphological characters in the published phylogenies. Hence, the question remains to what extent growth form characters can be used for the circumscription of monophyletic lineages.

Parmeliaceae is an ideal model to study the question of the importance of growth forms in the taxonomy of these fungi. This family includes morphologically very diverse lichens, including crustose (e.g., *Protoparmelia*; Henssen, 1995), peltate (e.g., *Omphalodiella*; Henssen, 1991), subcrustose (e.g., *Karoowia*; Hale, 1989), foliose (e.g., *Parmelia*; Elix, 1993), umbilicate (e.g., *Xanthomaculina*; Hale, 1985), fruticose (e.g., *Usnea*; Motyka, 1936) or subfruticose (e.g., *Almbornia*; Esslinger, 1981) species and even lichenicolous fungi devoid of any own photosynthetic partner, such as *Phacopsis* and *Nesolechia* (Persoh and Rambold, 2002), were placed here. Parmeliaceae includes approximately 2000 species in some 90 genera and represents the largest family within Lecanorales. The family belongs to the core of the Lecanorales closely related to other large families like the Lecanoraceae and Cladoniaceae (Wedin et al., 2000; Ekman and Tønsberg, 2002; Tehler et al., 2003; Lutzoni et al., 2004). This order is the most speciose within the class Lecanoromycetes which itself includes the bulk of lichen-forming fungi (Eriksson, 2006).

Based on different morphological characters, several genera were segregated at family level from Parmeliaceae. This includes Alectoriaceae, Anziaceae, Cetrariaceae, Corniculariaceae, Everniaceae, Hypogymniaceae, and Usnea-

ceae (Eriksson and Hawksworth, 1998). While most of these segregates were not used recently, Anziaceae, Hypogymniaceae, and Usneaceae have been accepted by some authors (e.g., Poelt, 1973; Elix and James, 1992; Golubkova, 1994; Wirth and Büdel, 1994; Kärnefelt et al., 1998; Stevens, 1999; McCarthy, 2003), based chiefly on deviating thallus morphology. Further, Alectoriaceae was accepted in several publications (Brodo, 1986; Esslinger, 1989; Eriksson and Hawksworth, 1992; Kärnefelt and Thell, 1992), mainly including taxa with deviating ascospores (Table 1). Based on similarities in micromorphological characters, such as a shared type of ascoma ontogeny and a characteristic structure in the ascoma anatomy, called a cupulate exciple, Henssen and Jahns (1973) accepted the morphologically diverse Parmeliaceae in a wider sense. In phylogenetic analyses based on molecular markers, all the proposed segregated families were shown to be nested within Parmeliaceae (Mattsson and Wedin, 1999; Wedin et al., 1999; Arup et al., 2007). Hence, currently a wider concept of Parmeliaceae is generally accepted (Eriksson, 2006).

Although molecular data supported a wider concept of Parmeliaceae, it is currently not clear if the different growth forms characterize natural groups within Parmeliaceae. Based on similarities in growth forms or micromorphological similarities (Table 1), different informal groupings have often been distinguished (Krog, 1982; Goward, 1985; Kärnefelt and Thell, 1992; Kärnefelt et al., 1992, 1998; Elix, 1993; Kärnefelt, 1998). These have usually been named after a characteristic genus e.g., parmelioid lichens, which share the typical foliose, dorsiventral growth form and laminal pycnidia and apothecia with the genus *Parmelia*, or cetrarioid lichens, which have erect foliose or subfruticose thalli with marginal apothecia and pycnidia like the genus *Cetraria*. Whether or not these groups represent monophyletic lineages remains to be investigated. In previous phylogenetic studies, a core group of parmelioid genera was found to be monophyletic (Crespo et al., 2001; Blanco et al., 2006), while Thell et al. (2004) failed to get support for parmelioid lichens as being monophyletic. In the latter study the parmelioid lichens fall into two separate groups, while a core group of cetrarioid lichens was supported as monophyletic. In the present study we addressed the question of phylogenetic patterns of the morphological variation observed in Parmeliaceae using a data set of 120 taxa using

Table 1
Morphologically defined groups in Parmeliaceae

Group	References	Main characteristics
Alectorioid (Alectoriaceae) s. lat.	Poelt (1973); Krog (1982); Esslinger (1989)	Thallus fruticose, cortical layer composed of periclinally arranged hyphae, sometimes additional layers present
Alectorioid (Alectoriaceae) s. str.	Eriksson and Hawksworth (1985); Kärnefelt and Thell (1992)	Thallus fruticose, ascospores pigmented, simple or septate to muriform
Anzioid (Anziaceae)	Poelt (1973)	Thallus foliose, asci polyspored, with curved ascospores
Cetrarioid	Goward (1985); Kärnefelt et al. (1992)	Thallus foliose to subfruticose, pycnidia and apothecia marginal
Hypogymnioid (Hypogymniaceae)	Poelt (1973)	Thallus foliose, lacking rhizines, medulla loose, often hollow
Parmelioid	Goward (1985); DePriest (1999)	Thallus foliose, pycnidia and apothecia laminal
Usneoid (Usneaceae)	Hale (1983); Kärnefelt et al. (1998)	Thallus fruticose, cortex para- and/or prosoplectenchymatous, never of periclinally arranged hyphae

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