Cryptic species in lichen-forming fungi

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Abstract: This contribution provides a synopsis of the presentations and discussions during the SIG session on cryptic speciation in lichen-forming fungi held during IMC9. In several cases, a re-examination of morphology against the background of molecular phylogenetic evidence revealed, sometimes subtle, morphological and/or chemical characters, supporting the distinction of particular clades at species level. However, there are also examples of cryptic species in which no morphological characters could be identified to distinguish between lineages. Several cases were presented in which distinct lineages are correlated with biogeographical patterns. When and how to name cryptic species was debated, and the use of terms such as "complex" or "aggregate" commended where the taxa formed part of a single lineage.

INTRODUCTION

The presentations at the session demonstrated that current species recognition in lichen forming-fungi vastly underestimates the true number of species. Based on phylogenetic and population studies, many cases were presented showing that numerous distinct lineages are hidden under a single species name. The issues raised can be grouped under the following headings: naming cryptic species, numbers of cryptic species, recognition of cryptic species, supporting species separations, and phylogeographic correlations. Collectively, these presentations provide a synopsis of the current state of knowledge of cryptic speciation in lichen-forming fungi.

NAMING CRYPTIC SPECIES

The recognition and naming of cryptic species from cryptic lineages was discussed and approaches and options were suggested. Hawksworth (2010) examined different groups as foraminifera, plant-pathogenic fungi, insects, and plants. The main species concepts were reviewed, and a pragmatic concept was proposed, defining a species as “groups of individuals separated by inheritable discontinuities and which it is useful to give a species name to” (Hawksworth 1996, 2010). The term cryptic species was circumscribed as “populations which are phylogenetically distinct and able to reproduce themselves, by sexual means or otherwise, but which are distinguished by molecular or other features that are either not evident macroscopically or generally overlooked” (Hawksworth 2010).

An increasing number of lichen-forming species are used as biomonitors or bioindicators of pollutants, environmental disturbance, or ecological continuity. Consequently there was the issue of how to proceed when cryptic species or lineages are found in taxa used in such studies where identifications need to be made quickly during field assessments – and access to a modern molecular laboratory is impractical. An acceptable way of referring to such groups of species was commended by Hawksworth (2010). The term “complex” or “aggregate” was supported as used when the populations are closely related, i.e. have a recent shared common ancestor. This practice is already familiar to and regularly used by botanists, citizen scientists, and ecologists dealing with complexes in plants, for example the Rubus fruticosus agg. and the Taraxacum officinale agg.

In some situations, however, the option of recognizing subspecies was suggested as perhaps the most appropriate solution, for example in paraphyletic populations (Figs 1 and 2) such as that of Parmelia pastillifera and P. tiliacea s. str. (Núñez-Zapata et al. 2010) (Fig. 1). In contrast, in cases where the cryptic taxa are not closely related but a result of convergence, i.e. they do not either occupy the same clade or have a recent common ancestor, it has to be recognized that the “complex” approach could give a misleading impression of affinity, as in Parmelina cryptotiliacea (Núñez Zapata et al. 2010) or lineages in Parmelia saxatilis (Divakar et al. 2010b).
There is a growing body of evidence that the approach to current species recognition in lichenized fungi, which is largely based on morphology and chemistry, vastly underestimates the number of phylogenetic species. Phylogenetic studies repeatedly indicate that numerous distinct lineages can be hidden under a single species name (Arguello et al. 2007, Baloch & Grube 2009, Grube & Kroken 2000, Kroken & Taylor 2001, Molina et al. 2004, Wirtz et al. 2008). In a number of cases, morphological or chemical differences have been interpreted as intraspecific variability. Re-examination of morphology against the background of a molecular phylogeny often reveals, sometimes subtle, and previously overlooked or viewed as unimportant, morphological and/or chemical characters, supporting the distinction of these clades at species level (Arguello et al. 2007, Divakar et al. 2005a, 2005b, Molina et al. 2004, Wirtz et al. 2008). However, there are also cases of cryptic species in which no morphological characters have yet been identified to distinguish distinct lineages. In several cases, distinct lineages are correlated with distinct biogeographical patterns (Arguello et al. 2007, Crespo et al. 2010, Molina et al. 2004, Wirtz et al. 2008). Phylogenetic studies identified distinct lineages that occur in different geographic regions, such as continents.

**RECOGNITION OF CRYPTIC SPECIES**

The large and increasing number of cryptic lineages detected in fungi means that the recognition of these lineages as separate taxa is a major issue of current fungal taxonomy.
those taxa are common. Thus, morphological identification of a lichen-forming species, sometimes even a genus, can be difficult. Therefore, cryptic taxa have been recognised historically in lichens, although not necessarily by that term. “The recognition and characterization of cryptic species is a burgeoning and exciting activity in current systematics, and a major challenge for mycologists of all kinds, not least lichenologists” (Hawksworth 2010). Suggestions for when to formally recognise species within cryptic lineages that are found in molecular studies were discussed (Muggia 2010, Pérez-Ortega & Printzen 2010), and a consensus of the session was to recognise species formally when the phylogeny was unequivocal and other evidence supported their separation, whether ultramicroscopic, “new” morphological, ecological (Muggia 2010) or geographical (Parmen et al. 2010) were discussed as examples for complementary evidence.

SUPPORTING SPECIES SEPARATIONS

Recent molecular phylogenies have supported some species separations that were previously based on subtle characters: for example, Parmelina carporrhizans and P. quercina (Argüello et al. 2007, Divakar et al. 2010b), Caloplaca aloczica and C. albopruinosa (Muggia 2010). It is also frequently found that distantly related major lineages show a surprising degree of morphological convergence. Examples of this phenomenon can be found within large families such as Parmeliaceae. For example, Parmelina and Austroparmelina were recently separated as independent genera based on geography and phylogeny. However, all species of Austroparmelina were previously included in concept of the genus Parmelina (Crespo et al. 2010, Divakar et al. 2010b). Also there are examples in microlichens, as in Capnodiales where the morphologically similar genera Racodium and Cystocoleus belong to independent lineages in recent phylogenetic studies (Muggia et al. 2008, Muggia 2010).

PHYLOGEOGRAPHIC CORRELATIONS

A number of lichen-forming species were historically thought to have wide distributions, including cosmopolitan and pantropical species. However, while that may be so for some species, molecular analyses have repeatedly demonstrated that many lineages can be hidden under a similar morphology. Several examples were discussed in the symposium (Divakar 2010, Muggia 2010, Parmen et al. 2010). Divakar et al. (2010) also found a correlation between reproductive modes and distribution patterns. In fertile species, cryptic lineages were frequently found, and geographically disjunct populations were discovered to represent different lineages (Divakar et al. 2010a). Several examples of this type were presented, including Melanelixia glabra and Parmelina quercina, two species distributed in areas with winter rain (Mediterranean climate) in North Africa, Europe and North America (Argüello et al. 2007, Divakar et al. 2010a, b). In sorediate taxa, cryptic

Fig. 2. Parmelina pastillifera (MAF 16473; upper) and P. tiliacea (MAF 16632; lower) both showing isidia, but in P. pastillifera they are peltate while in P. tiliacea are cylindrical. Bars = 5 mm.
lineages have also been found, but in this case the lineages can include specimens from different geographical regions; examples include *Flavoparmelia caperata*, *Parmotrema reticulatum*, and *P. tinctorum* (Divakar et al. 2005, 2010).

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