

Focus on lichenicolous fungi: Diversity and taxonomy under the principle “one fungus – one name”*

Josef HAFELLNER

Abstract: After introductory notes on subgroups of lichenicolous fungi, two issues, the diversity on various scales and the taxonomy under the rules of the Melbourne Code, are stressed.

On a global scale the diversity of lichenicolous fungi is still incalculable, as the inventory is still going on without any sign of reaching the end. On a regional and local scale lichenicolous fungi contribute about 10 to 20 percent to the total diversity of lichens and associated microfungi excluding the endolichenic fungi.

The consequences of recent changes in the International Code of Nomenclature are illustrated by two examples. In the light of recently gained insights by the application of molecular methods the taxonomy of *Lichenostigma* versus *Lichenothelia* including associated anamorphs is discussed as well as progress in the systematics of *Phoma*-like lichenicolous fungi.

1. Introduction

1.1. Lichenicolous fungi – various attempts at a definition

Lichenicolous fungi s. ampl. include all lichen-inhabiting fungi, both non-lichenized and lichenized, either obligate or facultative, with a colonization inducing symptoms on the host or not. In this broad circumscription the term comprises three subgroups.

1.1.1. Lichenicolous fungi s.str.

Lichenicolous fungi in the strict sense live exclusively on lichens. Most of them are non-lichenized but some are lichens that remain lichenicolous throughout their life cycle and thus clearly fulfill the definition (e.g. *Caloplaca magni-filii* and *Lecanora latro* on *Miriiquidica nigroleprosa*).

This is a good moment to remember the contribution of Josef POELT to what we know today about lichenicolous fungi. The lichenicolous lichens were one

* When in 1976 Prof. Josef POELT proposed a revision of *Karschia* at the borderline between lichenized and lichenicolous fungi for the author’s doctoral thesis, he also pointed out that in his experience, the decision which topic to focus on for a dissertation typically has a lasting impact on one’s scientific career. And so it happened. The present paper commemorates the 20th anniversary of Josef POELT’s death.

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of his favorite groups to study, and he described a number of them, namely in the genera *Caloplaca*, *Rhizocarpon*, *Lecidea* and *Lecanora*. He also compiled a first overview (POELT 1958) and was extremely interested in their autecology. He supervised two doctoral thesis projects concentrating on lichenicolous taxa, one completed by ZEHETLEITNER (1978) and the other that by the author (HAFELLNER 1979).

Some borderline cases make the delimitation of this group difficult, e.g. obligate youth parasites among lichenicolous lichens that might lose contact to their hosts on the one hand or even become independent and autonomous in later stages (e.g. *Miriquidica invadens* on *Sporastatia polyspora*, *Carbonea distans* on *Orphniospora mosigii*).

On the other hand a number of fungi, namely some basidiomycetes and anamorphic ascomycetes, are regularly found on lichens but may grow also on other substrate types, such as algal colonies, bryophytes or pure bark. We can call these fungi facultatively lichenicolous.

1.1.2. Endolichenic fungi

The endophytes of lichens (endolichenic fungi) are still little known and a study of them needs an approach applying molecular methods. An idea of their diversity at the local scale is provided by LI et al. (2007) who isolated 32 species, most of them widely distributed from 488 lichen thallus fragments gathered on a mountain in China. In a specific habitat bryophytes and lichens contain similar sets of endophytes (U'REN et al. 2010) and the species accumulation curve the authors published flattens at about 60 species. Diversity of large areas is significantly higher: in a study in which eight macrolichens originating from a geographic range between tropical Panama to arctic Canada were used for treatment, 630 endolichenic and 60 superficially adhering fungi were characterized by total genomic DNA data (ARNOLD et al. 2009). The authors regard the lichen microbiome as a key to understand the diversification of Ascomycota as well as the evolution of endophytism. Much of the diversity of endolichenic fungi results from primary non-lichenized lineages (Sordariomycetes, Dothideomycetes, Leotiomycetes and Pezizomycetes), with the majority of genotypes originating from Sordariomycetes – Xylariales.

1.1.3. Lichen epiphytes

Occasionally thalli of various lichens, often juvenile ones, can be found growing on or overgrowing other (macro)lichens. Usually they are harmless to their “host” substrate (e.g. *Hypogymnia physodes* on *Usnea* species, or *Leppraria* species on thalli of Parmeliaceae and *Umbilicaria* species).

But epiphytes may be very destructive when competing with other lichens. Strong competitors, such as *Pertusaria albescens*, can overgrow other bark epiphytes and kill parts or entire thalli of other lichens.

A number of microlichens live as facultative epiphytes on other lichens with various degrees of steadiness and the delimitation from the lichenicolous fungi s.str. becomes more and more difficult and blurred. Several species are occasionally found on other lichens (e.g. *Scoliciosporum umbrinum*, *Candelariella vitellina*), others more regularly (e.g. *Normandina pulchella* on lichens with cyanobacteria photobionts, a strain of *Rinodina olivaceobrunnea* on Lobariaceae) or only in young stages of development (e.g. *Calvitimela armeniacae* on *Sporastatia testudinea*).

2. Studying lichenicolous fungi – a flourishing field of mycology in recent decades

The study of lichenicolous fungi has a long tradition reaching back to the classical period of lichenology in the 19th century, when KÖRBER, Th. FRIES, NYLANDER, LEIGHTON and others described many of the more conspicuous and common taxa. In the 20th century, the number of both researchers and publications that appeared per year remained low until the 1980s (Fig. 1) when a period of intense research in lichenicolous fungi started and which is still continuing.

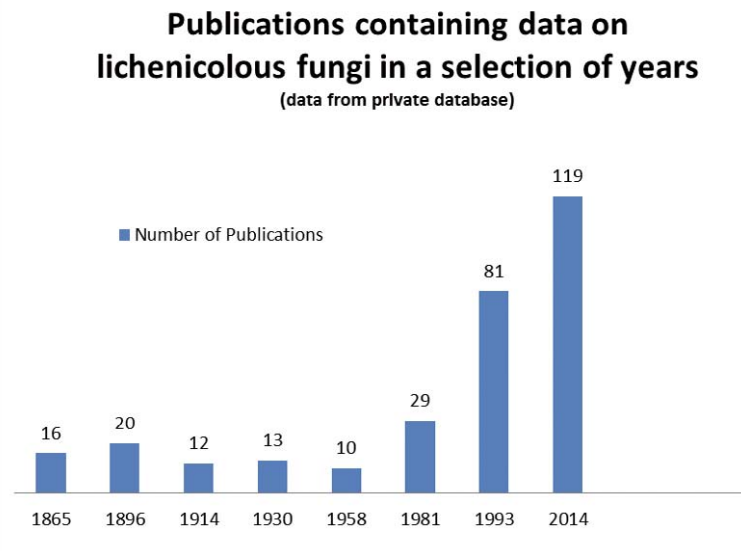


Fig. 1: Number of traced publications containing data on lichenicolous fungi (including lichenized taxa) in a selection of years in which important contributions to a better knowledge of lichenicolous fungi have appeared. The selected years refer to KÖRBER (1859–1865), ZOPF (1896), VOUAUX (1912–1914), KEISSLER (1930), POELT (1958), HAWKSWORTH (1981), SANTESSON (1993), ROUX et al. (2014) and BRACKEL (2014).

3. The diversity of lichenicolous fungi

The figures we get for the diversity of lichenicolous fungi depend highly on a number of parameters among which “geographic scale”, “subgroups included”, and “researcher involved” seem to be the most important.

In general, endolichenic fungi are not included in numerical values of diversity as they are not included in traditional mycofloristic studies but are a topic of their own. As the delimitation of lichenicolous epiphytes from lichenicolous fungi in the strict sense is diffuse, these species are partly counted and partly not. But as this is normally not a high number of species, the influence on the percentage values of lichenicolous fungi compared to the total lichen diversity is limited.

A much stronger influence on the reported diversity of localities or larger areas is exerted by the researchers performing the study. This is clearly indicated by the published results for larger areas with a relatively high species diversity in lichens but with very few lichenicolous fungi reported (e.g. DEBOLT & McCUNE 1993, PIERVITTORI & ISOCRONO 1999). At least in extra-tropical regions the experience is that areas with a high diversity in lichens also have a rich mycoflora of lichenicolous fungi (see below under 3.2. and 3.3.).

As for other groups of biota, the diversity of lichenicolous fungi can be calculated on various geographical scales: world-wide, regional or local.

3.1. Overall (global) diversity

Figures for the expected global diversity of lichenicolous fungi vary considerably depending on time and subgroups included. At the end of the millennium HAWKSWORTH and ROSSMAN (1997) gave the number of accepted species obligately growing on lichens as 894, of which 437 were described in the period 1976–1996. Now, more than 1,800 are already described (and accepted), and will rise eventually to about 3,000 in the future (HAWKSWORTH 2001, LAWREY & DIEDERICH 2003, 2015). A private database of the author for lichenicolous taxa contains so far 3224 heterotypic taxon entries on specific or infraspecific level excluding the endolichenic taxa.

The available data show that we are still far from knowing the total diversity of lichenicolous fungi on a worldwide scale. The taxon accumulation process is ongoing and there is no indication that we are close to reaching the plateau of the global species accumulation curve. On average, over the last two decades, 45 infrageneric taxa (mainly new species) were added per year, altogether c. 1,170 infrageneric taxa since 1990 (Fig. 2).

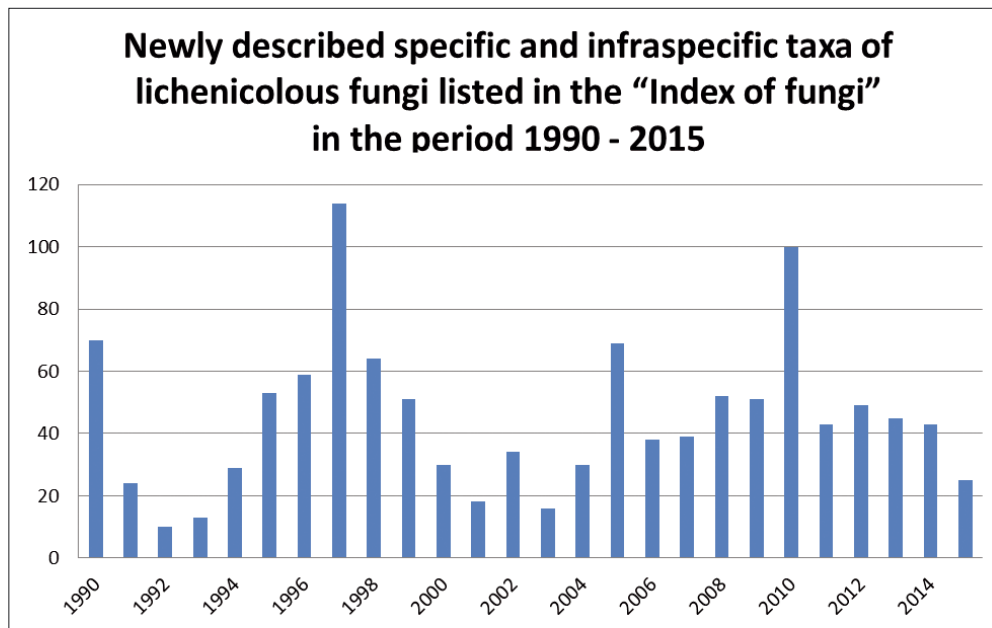


Fig. 2: Number of newly described specific and infraspecific taxa of lichenicolous fungi listed in the “Index of fungi” within the period 1990–2015 (sum of 2 issues per year). Exceptionally high numbers in the years 1990, 1997, 2005 and 2010 are caused by the appearance of major contributions in the years before, namely those by TRIEBEL (1989), DIEDERICH (1996), MATZER (1996), ETAYO (2002) and ETAYO & SANCHO GARCIA (2008).

There is no indication that revisions of larger genera/subgroups will considerably reduce the number of accepted species. Several larger revisions of lichenicolous fungal groups resulted in the reduction of some 10–20 % of the treated taxa to synonymy, but at the same time the detection of a comparable number of new species (Table 1).

A further topic concerning the number of accepted species, in general and also with lichenicolous taxa that are the focus of the present paper, are the new rules of nomenclature for fungi. As a result of the circumstance that several validly described lichenicolous deuteromycetes might be proven to represent anamorphic states of validly described teleomorphs we can expect that the number of accepted taxa will somewhat decline (ICN Art. 59, one fungus – one name, see below). But from the available data on species sets colonizing specific host lichens or host genera, it can be predicted that the decrease will not be dramatic, because candidates for teleomorphs and anamorphs constituting together genetically uniform holomorphs are relatively few.

Tab. 1: Balance of taxa resulting from revisional work in a selection of groups of lichenicolous fungi with various circumscriptions.

Group in focus	No. of accepted specific and infraspecific taxa treated in detail	No. of heterotypic taxa on specific and infraspecific level reduced to the synonymy	No. of newly described specific and infraspecific taxa	Reference
lichenicolous heterobasidiomycetes	48	0	41	DIEDERICH 1996
<i>Plectocarpon</i>	30 + 6	4	17	ERTZ et al. 2005
paraphysate hyalodidymospored pyrenomycetes	13 + 2	3	3	GRUBE & HAFELLNER 1990
paraphysate phaeo-amerospored pyrenomycetes	15 + 1	2	9	MATZER & HAFELLNER 1990
hyalo-amerospored pyrenomycetes	16 + 3	3	7	HOFFMANN & HAFELLNER 2000
ascomycetes with fissitunicate asci on foliicolous lichens	51 (excl. anamorphs)	3 (all representing anamorphs still separately treated)	36 (including 2 superfluous anamorphs)	MATZER 1996
ascomycetes on lecideoid lichens	47	32	10	TRIEBEL 1989

3.2. Regional diversity

The regional diversity of lichenicolous fungi can be calculated from “all taxa” checklists of more or less well known geographic entities. Such are available e.g. for Scandinavia + Finland (SANTESSON et al. 2004) or France (ROUX et al. 2014). Also more detailed floristic publications prepared with the aim to present more or less complete taxa lists for larger areas (mountain systems, national parks, etc.) give an impression of the regional diversity of lichenicolous fungi (Table 2). They usually summarize the results of many localities distrib-

uted over at least the major niches (bark, rock, soil) in a number of site types (various forest types, rocks of different mineral content, vegetation belts, various microclimatic stand characteristics) in which lichens and their lichenicolous fungi can grow. When such studies are conducted but lichenicolous fungi are neglected, this translates to possibly over 100 additional species being overlooked. Lichenicolous taxa contribute around 10–15 % to the total diversity of lichens and associated fungi and the values can go up to 20 % under favorable circumstances.

Tab. 2: Regional diversity of lichens, lichenicolous fungi and lichens as indicated by selected regional checklists.

Geographic area	Size [km ²]	Total diversity recorded (specific + infraspecific taxa)	Diversity of lichenicolous fungi including lichens	Diversity of lichenicolous fungi excl. lichenicolous lichens	Percentage of total diversity (rounded) all lichenicolous taxa / non-lichenized lichenicolous fungi	Source
Norway + Sweden +Finland	1,173,971	2968	513	430	17.3 / 14.5	SANTESSON et al. 2004
France	640,679	3528	696	513	19.7 / 14.5	ROUX et al. 2014
Belgium and Luxemburg	33,114	1,131	222	201	19.6 / 17.8	DIEDERICH & SÉRUSIAUX 2000
PN Cevennes (France)	2,297	1061	112	79	10.6 / 7.4	ROUX et al. 2008
Koralpe (Austria, Slovenia)	1,210	893	134	106	15.0 / 11.9	HAFELLNER 2008
Channel Islands NP (California)	900	504	57	48	11.3 / 9.5	KNUDSEN & KOCOURKOVÁ 2012
Klondike NHP (Alaska)	53	766	112	100	14.6 / 13.1	SPRIBILLE et al. 2010

A different approach was applied by FLEISCHHACKER et al. (2015) who investigated the diversity of lichenicolous fungi at a specific site type. At ten localities in the lower alpine belt of the Eastern Alps, saxicolous lichen communities were investigated using environmental amplicon sequencing (see publication for details). Field work yielded the detection of 46 lichenicolous fungi (excluding lichenothelioid taxa, lichenicolous lichens, and endolichenic fungi). Interplot similarity (beta-diversity) between two plots expressed with Sørensen indices ranged from 0.44 to 0.65. It is likely that the total diversity still has not been detected with the applied methods of field work. However, both the species accumulation curve (FLEISCHHACKER et al. 2015, Fig. 3b) and the application of the non-parametric estimator for species richness (CHAO 1987) to the observation-based data presented there (FLEISCHHACKER et al. 2015, Fig. 2) indicate that, for the specific investigated niche in the specific area, the taxon list of lichenicolous fungi is almost complete.

3.3. Local diversity

Taxon lists from single localities give an idea of the local diversity of lichenicolous fungi as they are usually prepared before the compilation of regional fungal floras. We used own field data of selected taxon-rich localities to illustrate average values of local diversity in total (lichens + lichenicolous fungi) compared to that of lichenicolous taxa alone (Table 3). The values are *grosso modo* similar to those in regional studies only somewhat lower.

Of considerable importance to the reported summarized diversity, at first of a locality and later on also on the results of a regional study, is the very different treatment of collected but unidentified species or even worse, of species recognized in the field but not collected by the researcher, because the researcher knows that he/she (and possibly also colleagues) will not be able to determine the specimen. Usually, these species are completely neglected and remain unmentioned and therefore are not part of all calculations. Only rarely they are treated in the same way as named taxa and are therefore counted too (see e.g. SPRIBILLE et al. 2010). Therefore it can be expected that the real diversity in the nature, local and regional, is some 20–40 % higher than reported even in well-performed studies.

Tab. 3: Local diversity of lichens, lichenicolous fungi and lichens calculated from taxa lists for individual localities.

Locality (country)	Site characteristics	Total diversity recorded (specific + infraspecific taxa) Excl. bark saprobes	Diversity of lichenicolous fungi including lichens	Diversity of lichenicolous fungi excl. lichenicolous lichens	Percentage of total diversity (rounded) all lichenicolous taxa / non-lichenized lichenicolous fungi	Data included in reference (locality no.)
Brandkogel (Austria)	marble and ground in tree line ecotone	89	10	10	11.2 / 11.2	WILFLING & HAFELLNER 2010a, b (SS01)
Handalpe (Austria)	Siliceous rocks and ground in tree line ecotone	128	19	9	14.8 / 7.0	HAFELLNER 2008 (St01) + additions
Lahnsattel (Austria)	old growth forest	146	20	20	13.7	HAFELLNER & KOMPOSCH 2007

4. Taxonomy of lichenicolous fungi under the principle “one fungus – one name“

The “Melbourne Code” or more precisely the “International Code of Nomenclature for algae, fungi, and plants” (McNEILL et al. 2012) brought four important changes affecting the work of taxonomists:

From 1 January 2012 on all taxonomists have the permission of electronic publication for all nomenclatural acts (ICN Art. 29) and are allowed to use either Latin or English for a diagnosis of a newly described taxon (ICN Art. 39.2).

From 1 January 2013 on mycotaxonomists face two further changes, first, that the publication of a new fungal name must include a citation of “an identifier issued by a recognized repository (e.g. Mycobank number)” in order to be validly published (ICN Art. 42), and second, that one of the principles of

the Code, that a taxon circumscribed in a particular way can have only one correct name, is extended to fungi (one fungus – one name; ICN Art. 59). As a consequence, since January 2013 all legitimate fungal names are treated equally for the purposes of establishing priority, regardless of the life history stage of the type. [Remember: in previous versions of the Code the corresponding Article allowed separate names for anamorphs and teleomorphs, whereas names for the whole fungus (holomorph) were typified by a teleomorph]. This is an important change and several authors have already published explaining comments (e.g. BRAUN 2012, GAMS et al. 2012, HAWKSWORTH 2011, 2012, HAWKSWORTH et al. 2013, MINNIS 2015, ROSSMAN 2014). For an introduction on how to validly apply the new rules, TURLAND (2013) should be consulted.

Since D.L. HAWKSWORTH started to investigate systematically anamorphic states of lichenicolous fungi in the late 1970s, many names, both generic and specific, have been validly published for anamorphs (asexual states) of lichenicolous fungi which now compete with names given to teleomorphs (sexual states) in the past. Very often the teleomorph names will prove to be the older ones. Every time when genetic identity between a named anamorph and a named teleomorph will be proven, the younger name will fall under the (usually heterotypic) synonymy of the name with priority, unless forms of protection are applied for illegitimate names in common use.

The impact of ICN Art. 59 on numerical diversity and correct naming of lichenicolous fungi is illustrated here with two examples, in which the author is involved in various ways, either by the description or the clarification of taxonomy and nomenclature of involved taxa.

Example 1: *Lichenostigma* and *Lichenothelia*: 1 or 2 genera?

In the early 1980s, the author described *Lichenostigma maureri*, a lichenicolous fungal genus and species which turned out to be extremely common, namely in the montane to subalpine vegetation belts of Holarctic orobiomes (HAFELLNER 1982). When a few years later, we described *Phaeosporobolus usneae* (HAWKSWORTH & HAFELLNER 1986), an anamorphic fungus with similar ecology and distribution and often co-occurring with *Lichenostigma maureri*, we pointed already to the anatomical and ecological similarities between the “two” fungi. At that time it was in accordance with the Code to give an anamorphic state a separate name.

Recently, ERTZ et al. (2014) showed that the type species of the two genera are genetically identical, and following the new Art. 59 of ICN, *Phaeosporobolus* (1986) has been reduced under the synonymy of *Lichenostigma* (1982) as has been *Phaeosporobolus usneae* under *Lichenostigma maureri*. Consequently, *Phaeosporobolus* species for which the genetically identical teleomorph has not yet been described (e.g. *Phaeosporobolus alpinus*) were trans-

ferred to *Lichenostigma*. In a phylogenetic tree, *Lichenostigma* species form a separate clade in Arthoniomycetes with a rather isolated position. Therefore the authors decided to describe an order Lichenostigmatales (ERTZ et al. 2014).

Related to this is the case of *Lichenothelia*. Species assigned to *Lichenothelia* (type species not yet sequenced) develop thalloconidia-like anamorphic states (HENSSEN 1987) and simultaneously often pycnidia containing microconidia. Fortunately, as far as we know, anamorphs of *Lichenothelia* have not been named so far and therefore when searching for legitimate names of *Lichenothelia* species, no anamorph names need to be considered. The *Lichenothelia* species so far sequenced come out as a clade in Dothideomycetes (ERTZ et al. 2014). Several *Lichenostigma* species, many of those connected to composite superficial hyphal strands, are obviously more closely related to the sequenced *Lichenothelia* species. But as long as the type species, *L. scopularia*, exhibiting some morphoanatomic characters not found in any of the other species assigned to the genus, is not characterized by DNA data, it would not be serious to propose the corresponding combinations.

Example 2: Progress in the taxonomy of *Phoma*-like lichenicolous fungi

Phoma (1880) is a large (more than 3,000 infrageneric taxa described) morphoanatomically characterized genus of ascomycete anamorphs with nine sections, which have already been demonstrated to be polyphyletic in part. *Phoma* SACC. s.str. is a conserved name, with *P. herbarum* as type species which, in phylogenetic analyses of DNA data, comes out in the Didymellaceae clade (DE GRUYTER et al. 2009, AVESKAMP et al. 2010). Other *Phoma* species turn up in several other clades.

About 50 lichenicolous fungi have been assigned to *Phoma* in the past but it has not been possible to demonstrate congenerity with the type species, *P. herbarum*, for any of them. Consequently *Phoma*-like lichenicolous fungi most probably do not represent anamorphs of *Didymella* or related genera in Didymellaceae.

Several genera have already been described for *Phoma*-like lichenicolous fungi, e.g. *Bachmanniomyces*, *Briancoppinsia*, *Diederichia*, *Diederichomyces*, *Pseudoseptoria*, *Lichenosticta* and *Vouauxiomyces*. The phylogenetic position of some of these genera as well as of a considerable number of lichenicolous “*Phoma*” species is still unknown due to the lack of molecular data but for some others sequence data are already available and their phylogeny can be reconstructed.

A well-known genus of lichenicolous fungi easy to recognize on the genus level is *Abrothallus* (1845). Occasionally, *Abrothallus* ascomata co-occur with a *Phoma*-like anamorphic state but with peculiar truncate conidia. In other cases such anamorphs with a corresponding set of characters may also occur

alone. These anamorphs were partly described in *Phoma*, but later the genus *Vouauxiomyces* (1979) was created for them (HAWKSWORTH & DYKO 1979). Several of these asexual states have in the meantime been confirmed to constitute anamorphs of already named *Abrothallus* species (SUIJA et al. 2015). Such species of *Vouauxiomyces* have accordingly been reduced to synonymy under genetically identical *Abrothallus* species, or, if the genetically identical teleomorph has not yet been described, the anamorphic names need to be combined into *Abrothallus*. Anamorphs recognized to represent undescribed species are, following ICN Art. 59, described in *Abrothallus* and not in *Vouauxiomyces* although in such a case the diagnosis logically does not mention character states of the teleomorph. Furthermore the recently introduced *Epinephroma kamchatica* (ZHURBENKO et al. 2012), type of the genus *Epinephroma* (2012) turned out to be the anamorph of an *Abrothallus* (SUIJA et al. 2015b). Another interesting question is the phylogenetic position of *Abrothallus* for which a relationship with Arthoniales was discussed in the past. PÉREZ-ORTEGA et al. (2013) have shown that the clade belongs to the Dothideomycetes, a fungal class in which the *Abrothallus-Vouauxiomyces*-clade is rather isolated. The authors correspondingly decided to introduce the order Abrothallales, sister to Jahnulales and on a branch together with Patellariales.

A lichenicolous *Phoma*-like fungus infesting a wide range of parmeliaceous macrolichens is *Phoma cytospora*. It is relatively easy to determine because of its peculiar rod-shaped conidia. DIEDERICH et al. (2012) managed to sequence that fungus and the phylogenetic analysis has shown that it represents the anamorph of an arthonialean fungus with a hitherto unknown teleomorph. The support values for the branching of the cladogram indicate that the fungus is evidently not congeneric with one of the other accepted genera in Arthoniales. Therefore the authors have described it as a new genus, *Briancoppinsia* (2012).

LAWREY et al. (2012) were able to show that several other lichenicolous *Phoma*-like fungi represent members of Phaeosphaeriaceae. In a premature act TRAKUNYINGCHAROEN et al. (2014) described a genus for these species, *Diederichomyces* (2014). We were able to demonstrate that these asexual fructifications represent anamorphs of ascomycetes, for which *Didymocyrtis* (1921) turned out to be the oldest legitimate generic name (ERTZ et al. 2015). Species of *Phoma* coming out in this clade (Dothideales-Phaeosphaeriaceae) were reduced to synonymy under genetically identical *Didymocyrtis* species, or if the genetically identical teleomorph has not yet been found or described, the *Phoma* names needed to be combined into *Didymocyrtis*. Furthermore, our results indicate a considerable variation in ascospore septation and size of conidia, because *Didymocyrtis* species may be phragmosporous (*D. ramalinae*) or even dictyosporous (*D. physciae*) instead of didymosporous (*D. consimilis*, type), and the conidia can be very large and *Macrophoma*-like (*Didymocyrtis pseudeverniae*, generic type of *Diederichia*).

5. Conclusions

We can expect a further considerable increase of newly detected species and the recognition of further genera by the application of molecular methods. The decision to create a further genus should however be taken with caution, because generic names may already exist for many of them, hidden in the traditional generic synonymy. A broad and thorough investigation of the nomenclature is in all the cases highly recommended.

On account of the still unclear phylogenetic position of the majority of the genera containing lichenicolous species it is practically not serious any more to describe a further fungal genus, namely for anamorphs, as long as its phylogeny is not clarified.

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7. References

- ARNOLD, A.E., MIADLIKOWSKA, J., HIGGINS, K.L., SARVATE, S.D., GUGGER, P., WAY, A., HOFSTETTER, V., KAUFF, F. & LUTZONI, F. 2009: A phylogenetic estimation of trophic transition networks for ascomycetous fungi: are lichens cradles of symbiotrophic fungal diversification? — *Syst. Biol.* **58**: 283–297.
- AVESKAMP, M.M., GRUYTER, J. DE, WOUDEBERG, J.H.C., VERKLEY, G.J.M. & CROUS, P. W. 2010: Highlights of the Didymellaceae: A polyphasic approach to characterise *Phoma* and related pleosporalean genera. — *Stud. Mycol.* **65**: 1–60.
- BRACKEL, W. VON 2014: Kommentierter Katalog der flechtenbewohnenden Pilze Bayerns. — *Biblioth. Lichenol.* **109**: 1–476.
- BRAUN, U. 2012: The impacts of the discontinuation of dual nomenclature of pleomorphic fungi: the trivial facts, problems, and strategies. — *IMA Fungus* **3**: 81–86.
- CHAO, A. 1987: Estimating the population size for capture-recapture data with unequal catchability. — *Biometrics* **43**: 783–791.
- DEBOLT, A. & McCUNE, B. 1993: Lichens of Glacier National Park, Montana. — *Bryologist* **96**: 192–204.
- DIEDERICH, P. 1996: The lichenicolous heterobasidiomycetes. — *Biblioth. Lichenol.* **61**: 1–198.
- DIEDERICH, P., LAWREY, J. D., SIKAROODI, M., BOOM, P. VAN DEN & ERTZ, D. 2012: *Brianco-ppinsia*, a new coelomycetous genus of Arthoniaceae (Arthoniales) for the lichenicolous *Phoma cytospora*, with a key to this and similar taxa. — *Fung. Diversity* **52**: 1–12.

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- ERTZ, D., CHRISTNACH, C., WEDIN, M. & DIEDERICH, P. 2005: A world monograph of the genus *Plectocarpon* (Roccellaceae, Arthoniales). — *Biblioth. Lichenol.* **91**: 1–155.
- ERTZ, D., LAWREY, J.D., COMMON, R.S. & DIEDERICH, P. 2014: Molecular data resolve a new order of Arthoniomycetes sister to the primarily lichenized Arthoniales and composed of black yeasts, lichenicolous and rock-inhabiting species. — *Fung. Diversity* **66**: 113–137.
- ERTZ, D., DIEDERICH, P., LAWREY, J.D., BERGER, F., FREEBURY, C.E., COPPINS, B., GARDIENNET, A. & HAFELLNER, J. 2015: Phylogenetic insights resolve Dacampiaceae (Pleosporales) as polyphyletic: *Didymocyrtis* (Pleosporales, Phaeosphaeriaceae) with *Phoma*-like anamorphs resurrected and segregated from *Polycoccum* (Trypetheliales, Polycoccaceae fam. nov.). — *Fung. Diversity* **74**: 53–89.
- ETAYO, J. 2002: Aportación al conocimiento de los hongos liquenícolas de Colombia. — *Biblioth. Lichenol.* **84**: 1–154.
- ETAYO, J. & SANCHO GARCÍA, L. 2008: Hongos liquenícolas del Sur de Sudamérica, especialmente de Isla Navarino (Chile). — *Biblioth. Lichenol.* **98**: 1–302, tab.
- FLEISCHHACKER, A., GRUBE, M., KOPUN, T., HAFELLNER, J. & MUGGIA, L. 2015: Community analyses uncover high diversity of lichenicolous fungi in alpine habitats. — *Microb. Ecol.* **70**: 348–360.
- GAMS, W., HUMBER, R.A., JAKLITSCH, W., KIRSCHNER, R. & STADLER, M. 2012: Minimizing the chaos following the loss of Article 59: Suggestions for a discussion. — *Mycotaxon* **119**: 495–507.
- GRUBE, M. & HAFELLNER, J. 1990: Studien an flechtenbewohnenden Pilzen der Sammelgattung *Didymella* (Ascomycetes, Dothideales). — *Nova Hedwigia* **51**: 283–360.
- GRUYTER, J. DE, AVESKAMP, M.M., WOUDEBERG, J.H.C., VERKLEY, G.J.M., GROENEWALD, J.Z. & CROUS, P.W. 2009: Molecular phylogeny of *Phoma* and allied anamorph genera: Towards a reclassification of the *Phoma* complex. — *Mycol. Res.* **113**: 508–519.
- HAFELLNER, J. 1979: *Karschia* – Revision einer Sammelgattung an der Grenze von lichenisierten und nicht lichenisierten Ascomyceten. — *Nova Hedwigia, Beih.* **62**: 1–248.
- HAFELLNER, J. 1982: Studien über lichenicole Pilze und Flechten II. *Lichenostigma maureri* gen. et spec. nov., ein in den Ostalpen häufiger lichenicoler Pilz (Ascomycetes, Arthoniales). — *Herzogia* **6**: 299–308.
- HAFELLNER, J. 2008: Zur Diversität lichenisierter und lichenicoler Pilze im Gebiet der Koralpe (Österreich: Kärnten und Steiermark, Slowenien). — *Mitt. Naturwiss. Vereins Steiermark* **138**: 29–112.
- HAFELLNER, J. & KOMPOSCH, H. 2007: Diversität epiphytischer Flechten und lichenicoler Pilze in einem mitteleuropäischen Urwaldrest und einem angrenzenden Forst. — *Herzogia* **20**: 87–113.
- HAWKSWORTH, D.L. 1981: The lichenicolous Coelomycetes. — *Bull. Brit. Mus. (Nat. Hist.), Bot.* **9/1**: 1–98.
- HAWKSWORTH, D.L. 1991: The fungal dimension of biodiversity: magnitude, significance, and conservation. — *Mycol. Res.* **95**: 641–655.

- HAWKSWORTH, D.L. 2001: The magnitude of fungal diversity: the 1.5 million species estimate revisited. — *Mycol. Res.* **105**: 1422–1432.
- HAWKSWORTH, D.L. 2011: A new dawn for the naming of fungi: impacts of decisions made in Melbourne in July 2011 on the future publication and regulation of fungal names. — *IMA Fungus* **2**: 155–162.
- HAWKSWORTH, D.L. 2012: Managing and coping with names of pleomorphic fungi in a period of transition. — *IMA Fungus* **3**: 15–24.
- HAWKSWORTH, D.L. & DYKO, B.J. 1979: *Lichenodiplis* and *Vouauxiomyces*: two new genera of lichenicolous Coelomycetes. — *Lichenologist* **11**: 51–61.
- HAWKSWORTH, D.L. & HAFELLNER, J. 1986: *Phaeosporobolus usneae*, a new and widespread lichenicolous deuteromycete. — *Nova Hedwigia* **43**: 525–530.
- HAWKSWORTH, D.L. & ROSSMAN, A.Y. 1997: Where are all the undescribed fungi? — *Phytopathology* **87**: 888–891.
- HAWKSWORTH, D.L., MCNEILL, J., DE BEER, Z.W. & WINGFIELD, M.J. 2013: Names of fungal species with the same epithet applied to different morphs: how to treat them. — *IMA Fungus* **4**: 53–56.
- HENSSEN, A. 1987: *Lichenothelia*, a genus of microfungi on rocks. — In PEVELING, E. (ed.): *Progress and problems in lichenology in the Eighties*. — *Biblioth. Lichenol.* **25**: 257–293.
- HOFFMANN, N. & HAFELLNER, J. 2000: Eine Revision der lichenicolen Arten der Sammelgattungen *Guignardia* und *Physalospora* (Ascomycotina). — *Biblioth. Lichenol.* **77**: 1–181, tab.
- KEISSLER, K. VON 1930: Die Flechtenparasiten. — In: Dr. L. RABENHORST's Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, 2. Aufl., **8**: I–XI, 1–712. — Leipzig: Akademische Verlagsgesellschaft.
- KNUDSEN, K. & KOCOURKOVÁ, J. 2012: The annotated checklist of lichens, lichenicolous and allied fungi of Channel Islands National Park. — *Opuscula Philolichenum* **11**: 145–302.
- KOERBER, G.W. 1859–1865: *Parerga lichenologica. Ergänzungen zum Systema lichenum Germaniae*. — Breslau: Trewendt. (1859: 1–96, 1860: 97–192, 1861: 193–288, 1863: 289–384, 1865: 385–501, I–XVI).
- LAWREY, J.D. & DIEDERICH, P. 2003: Lichenicolous fungi: Interactions, evolution, and biodiversity. — *Bryologist* **106**: 80–120.
- LAWREY, J.D. & DIEDERICH, P. 2015: Lichenicolous fungi – worldwide checklist, including isolated cultures and sequences available. — (<http://www.lichenicolous.net>)
- LAWREY, J.D., DIEDERICH, P., NELSEN, M.P., FREEBURY, C., VAN DEN BROECK, D., SIKAROODI, M. & ERTZ, D. 2012: Phylogenetic placement of lichenicolous *Phoma* species in the Phaeosphaeriaceae (Pleosporales, Dothideomycetes). — *Fung. Diversity* **55**: 195–213.
- LI, W.C., ZHOU, J., GUO, S.Y. & GUO, L.D. 2007. Endophytic fungi associated with lichens in Baihua mountain of Beijing, China. — *Fung. Diversity* **25**: 69–80.

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- MATZER, M. 1996: Lichenicolous ascomycetes with fissitunicate asci on foliicolous lichens. — *Mycol. Pap.* 171: I–X, 1–202.
- MATZER, M. & HAFELLNER, J. 1990: Eine Revision der lichenicolen Arten der Sammelgattung *Rosellinia* (Ascomycetes). — *Biblioth. Lichenol.* 37: 1–138, tab.
- MCNEILL, J.N., BARRIE, F.R., BUCK, W.R., DEMOULIN, V., GREUTER, W., HAWKSWORTH, D. L., HERENDEEN, P.S., KNAPP, S., MARHOLD, K., PRADO, J., PRUD'HOMME VAN REINE, W.F., SMITH, G.F., WIERSEMA, J.H. & TURLAND, N.J. 2012: International Code of Nomenclature for algae, fungi, and plants (Melbourne Code). — *Regnum Veg.* 154: 1–208. — Koenigstein: Koeltz Scientific Books. (<http://www.iapt-taxon.org/nomen/main.php>)
- MINNIS, A.M. 2015: The shifting sands of fungal naming under the ICN and the one name era for fungi. — In McLAUGHLIN, D.L. & SPATAFORA, J.W. (eds.): *The Mycota*. Vol. VII (B). Systematics and Evolution. 2nd ed., p. 179–203. — Berlin, Heidelberg: Springer.
- PÉREZ-ORTEGA, S., SUIJA, A., CRESPO, A. & DE LOS RÍOS, A. 2014: Lichenicolous fungi of the genus *Abrothallus* (Dothideomycetes: Abrothallales ordo nov.) are sister to the predominantly aquatic Jahnulales. — *Fung. Diversity* 64: 295–304.
- PIERVITTORI, R. & ISOCRONO, D. 1999: I licheni della Valle d'Aosta – I. Indagine bibliografica e aspetti storici (1764–1998). — Aosta: Museo Regionale di Scienze Naturali Saint-Pierre, Monografie 1: 1–264.
- POELT, J. 1958: Über parasitische Flechten. II. — *Planta* 51: 288–307.
- ROSSMAN, A.Y. 2014: Lessons learned from moving to one scientific name for fungi. — *IMA Fungus* 5: 81–89.
- ROUX, C., COSTE, C., BRICAUD, O., BAUVET, C. & MASSON, D. 2008: Lichens et champignons lichénicoles du parc national des Cévennes (France). 5 — Vue d'ensemble et conclusion. — *Bull. Soc. Linn. Provence* 59: 243–279.
- ROUX, C., MONNAT, J.-Y., VAN HALUWYN, C., CHIPON, B., POUMARAT, S., HOUMEAU, J.-M., DIEDERICH, P., MASSON, D., CARLIER, G., BERTRAND, M., BOISSIÈRE, J.-C., BAUVET, C., LAGRANDE, J., BRICAUD, O., GARDIENNET, A., DERRIEN, M.-C., MÉNARD, T., FAROU, J.-L., BLONDEL, È., GUILLOUX, F., LORELLA, B., NAVARRO-ROSINÉS, P., ESNAULT, J., GUEIDAN, C., BOISSIER, X., AGNELLO, G., FRANCHON, C., OFFERHAUS, B., SUSSEY, J.-M., ASTA, J., MASSÉ, L. J.-C., LOHÉZIC-LE DÉVÉHAT, F., DAVOUST, M., QUELEN, Y., GONNET, D., GONNET, O., FERREZ, Y., MARTIN, B., MARTIN, J.-L., VAUDORÉ, D., RAGOT, R., BOUMIER, R., RÉMY, C., WIRTH, V., DUFRÈNE, P., ENGLER, R., LACOUX, D., SCHMITT, A., CLERC, P., MARY, F.J., MARY, J., VERMEULEN, J.-C., MONTAVONT, J.-P., GAVÉRIAUX, J.-P., DEMEULANT, J., BÉGUINOT, J., VALLADE, J., CHAPUIS, L., HUGUENY, P., LERAT, C., MAGGI, F., BAUBET, R., DROUARD, F., SÉRUSIAUX, E., DESCHÂTRES, R. & HAIRIE, F. [«ROUX, C. et coll.»] 2014: Catalogue des lichens et champignons lichénicoles de France métropolitaine. — Fougères: Éditions d'art, Henry des Abbayes.
- SANTESSON, R. 1993: The lichens and lichenicolous fungi of Sweden and Norway. — Lund: SBT-förlaget.
- SANTESSON, R., MOBERG, R., NORDIN, A., TØNSBERG, T. & VITIKAINEN, O. 2004: Lichen-forming and lichenicolous fungi of Fennoscandia. — Uppsala: Museum of Evolution, Uppsala University.

- SPRIBILLE, T., PÉREZ-ORTEGA, S., TØNSBERG, T. & SCHIROKAUER, D. 2010: Lichens and lichenicolous fungi of the Klondike Gold Rush National Historic Park, Alaska, in a global biodiversity context. — *Bryologist* **113**: 439–515.
- SUIJA, A., DE LOS RÍOS, A. & PÉREZ-ORTEGA, S. 2015: A molecular reappraisal of *Abrothallus* species growing on lichens of the order Peltigerales. — *Phytotaxa* **195**: 201–226.
- TRAKUNYINGCHAROEN, T., LOMBARD, L., GROENEWALD, J.Z., CHEEWANGKON, R., TOANUN, C., ALFENAS, A.C. & CROUS, P.W. 2014: Mycoparasitic species of *Sphaerellopsis*, and allied lichenicolous and other genera. — *IMA Fungus* **5**: 391–414.
- TRIEBEL, D. 1989: Lecideicole Ascomyceten. Eine Revision der obligat lichenicolen Ascomyceten auf lecideoiden Flechten. — *Biblioth. Lichenol.* **35**: 1–278.
- TURLAND, N.J. 2013: The Code decoded: a user's guide to the International Code of Nomenclature for algae, fungi, and plants. — *Regnum Veg.* **155**: 1–169.
- U'REN, J.M., LUTZONI, F., MIADLIKOWSKA, J. & ARNOLD, A.E. 2010: Community analysis reveals close affinities between endophytic and endolichenic fungi in mosses and lichens. — *Microb. Ecol.* **60**: 340–353.
- VOUAUX, L. 1912–1914: Synopsis des champignons parasites de lichens. — *Bull. Soc. Mycol. France* 1912, **28**: 177–256; 1913, **29**: 33–128, 399–446, 447–494; 1914, **30**: 135–198, 281–329.
- WILFLING, A. & HAFELLNER, J. 2010a: Lichen diversity on marble outcrops at high altitudes in the Eastern Alps (Austria). — In HAFELLNER, J., KÄRNEFELT, I. & WIRTH, V. (eds.): Diversity and ecology of lichens in polar and mountain ecosystems. — *Biblioth. Lichenol.* **104**: 339–371.
- WILFLING, A. & HAFELLNER, J. 2010b: Zur Diversität der Flechten und lichenicolen Pilze auf Böden über Marmor in den Hochlagen der Ostalpen (Österreich). — *Mitt. Naturwiss. Vereins Steiermark* **140**: 85–120.
- ZEHETLEITNER, G. 1978: Über einige parasitische Arten der Flechtengattung *Verrucaria*. — *Nova Hedwigia* **29**: 683–734.
- ZHURBENKO, M.P., HIMELBRANT, D.E., KUZNETSOVA, E.S. & STEPANCHIKOVA, I.S. 2012: Lichenicolous fungi from Kamchatka Peninsula, Russia. — *Bryologist* **115**: 295–312.
- ZOPF, W. 1896: Uebersicht der auf Flechten schmarotzenden Pilze. — *Hedwigia* **35**: 312–366.

Address of the author:

Prof. Dr. Josef HAFELLNER
 Institut für Pflanzenwissenschaften, NAWI Graz, Karl-Franzens-Universität Graz
 Holteigasse 6, 8010 Graz, Austria
 Email: josef.hafellner@uni-graz.at

