The Bryologist 106(1), pp. 80–120

INVITED ESSAY

New Frontiers in Bryology and Lichenology

Lichenicolous Fungi: Interactions, Evolution, and Biodiversity

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Abstract. *The lichenicolous fungi represent an important ecological group of species that form obligate associations with lichens. They have been studied seriously for over 200 years and the European species are especially well collected. However, collecting in other areas has been far less systematic and many new species await discovery. North American species are especially under-studied and this review is intended to stimulate the collection and study of these species. To encourage this study by lichenologists, we review the sorts of interactions formed by lichenicolous fungi with their lichen hosts, discuss various aspects of host specificity, virulence, chemical ecology, and evolution of lichenicolous fungi and provide a complete taxonomic listing of lichenicolous genera arranged as far as possible into natural groupings. In each section we suggest research topics in need of further study, and provide a listing of significant literature. We hope by calling attention to the largely unexplored biodiversity of lichenicolous fungi, investigators will take up the study of these fascinating organisms.*

Lichenicolous fungi are a highly specialized and successful group of organisms that develop on lichens and form with them three- or sometimes four to five-membered associations. They are relatively inconspicuous and are rarely collected by non-lichenologists. Lichenologists in the past were not much interested in these fungi, perhaps owing to their lack of knowledge of non-lichenized fungi. Professional mycologists who would have been knowledgeable of the groups rarely studied this very specialized substrate. For these reasons, lichenicolous fungi were poorly known until recently.

One of the first examples of a lichenicolous fungus studied, described, and illustrated is *Biatoropsis usnearum*, a heterobasidiomycete forming large gall-like structures on thalli of *Usnea*. Dillenius (1742) illustrated two species of the *Usnea barbata* group in the *Historia Muscorum*, one of them bearing numerous '*orbiculos*', which clearly represent basidiomata of the fungus. In 1795, Acharius discussed and illustrated *Usnea* specimens infected by *B. usnearum* (Fig. 1), and in 1810 he published fine color illustrations of this fungus.

During the 19th century, many more species of lichenicolous fungi were described, and Lindsay (1869) presented a first overview of the group. Zopf (1896) also gave a list of lichen hosts, with an enumeration of the fungi present on each of them. Olivier (1905–1907) provided a detailed account of the lichenicolous fungi from France, and Vouaux (1912–1914) published a worldwide flora with keys and descriptions of all known species. Keissler (1930) revised the central European species. These works by Vouaux and Keissler represent invaluable information still useful today. More recent compilations were given by Clauzade and Roux (1976 – with 457 species) and Clauzade et al. (1989 – with 686 species).

Hawksworth (1983) published keys to 218 lichenicolous species known from the British Isles, and these keys stimulated many lichenologists to study this fascinating group of fungi. Entire revisions of three major groups became available, the lichenicolous hyphomycetes (Hawksworth 1979), the lichenicolous coelomycetes (Hawksworth 1981), and the lichenicolous heterobasidiomycetes (Diederich 1996). During the past 10 years, and especially since the publication of Santesson's (1993) *The Lichens and Lichenicolous Fungi of Sweden and Norway*, lichen checklists of many European countries appeared, and most of them include lichenicolous fungi. This encouraged many lichenologists to col-

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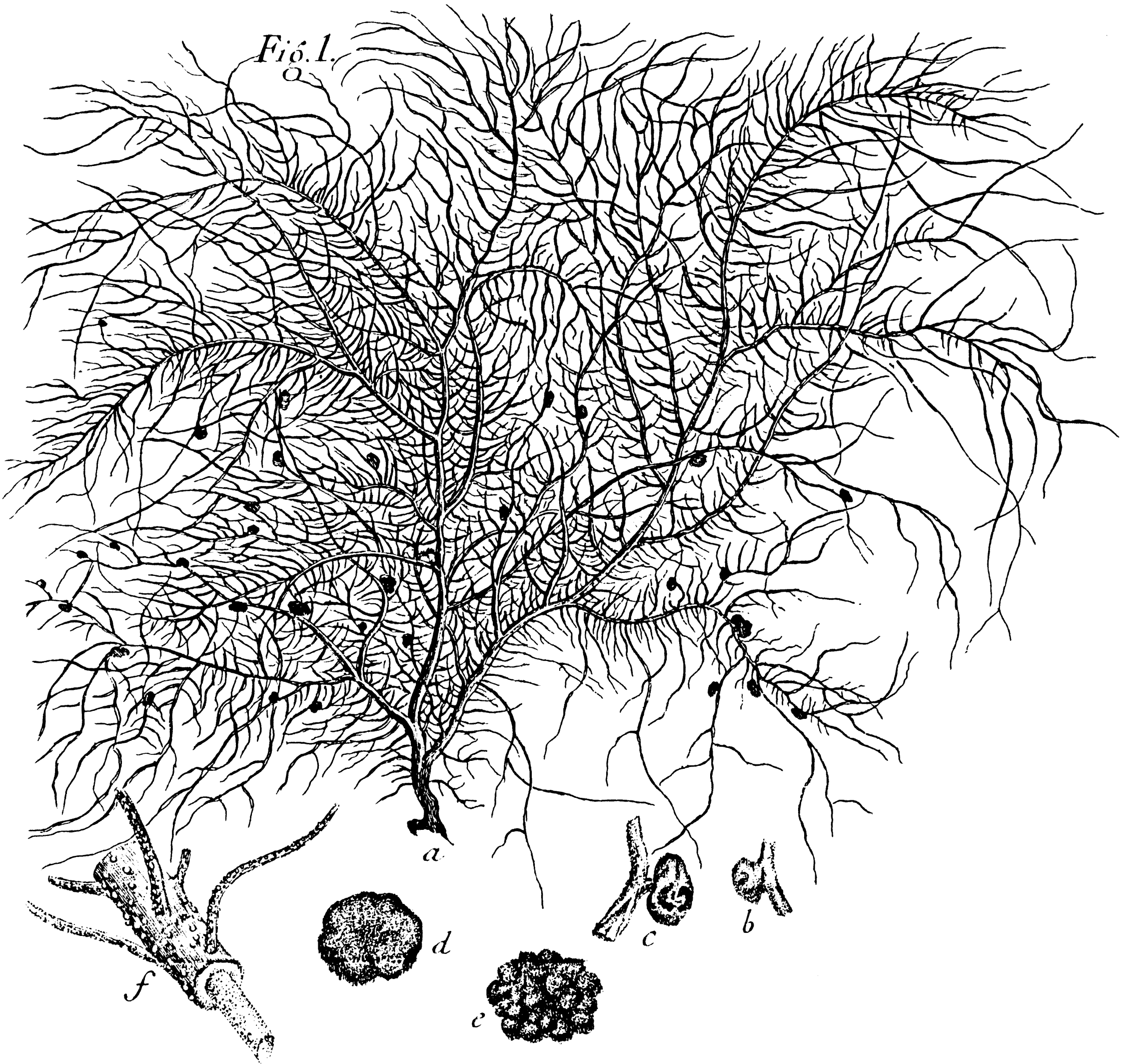

FIGURE 1. The lichenicolous heterobasidiomycete *Biatoropsis usnearum* that forms abundant gall-like basidiomata on the thallus of *Usnea* spp., as depicted by Acharius (1795).

lect and study these organisms, and never before have so many publications on them appeared and so many new species described. Since 1989, the date of the latest worldwide compilation (Clauzade et al. 1989), the number of species has approximately doubled, and this trend is in no way diminishing, as exemplified by Etayo's recent work on Colombia, in which he describes 41 new species and enumerates many more specimens that could not be identified (Etayo 2002).

There are two main objectives of the present paper. Firstly, we wish to give a general overview of current knowledge on lichenicolous fungi, focusing on aspects that have often been neglected in the past. Along with this discussion we offer a number of hypotheses for testing. Secondly, we propose a systematic arrangement for all lichenicolous fungi. This is a more or less complete list of all genera, which makes it an important update to Clauzade et al. (1989). It includes numbers of species per genus, which indicates for the first time since 1989 the number of known lichenicolous species, and for each genus we provide references to important taxonomic papers.

INTERACTIONS OF LICHENICOLOUS FUNGI WITH LICHENS

Fungi commonly associate with lichen thalli in nature, but these associations are rather loose and non-specific in many cases. By definition, lichenicolous fungi form obligate associations with lichens, either as saprotrophs that colonize dead lichen thalli, or parasites that obtain fixed carbon from living lichen hosts in some way (Hawksworth 1982*c*, 1988*c,d*). Parasites range from relatively nonaggressive, commensalistic forms that cause no obvious damage to aggressively virulent types that cause obvious lesions or discolorations. There are also lichenicolous lichens that colonize a separate lichen host and maintain a separate photobiont.

These interactions have rarely been investigated sufficiently to answer even the most basic questions. Little or nothing is known about the modes of cellular contact, nutrient exchange, antibiosis, or virulence. The degree of host-specificity is usually not known for certain, so whatever basis there is for any presumed host specificity is also unknown. Very few lichenicolous fungi have ever been brought into axenic culture, so little is known about their cultural requirements; for the same reason, controlled experiments involving fungal cultures have only rarely been done in the laboratory. In this section, we briefly discuss possible fungal interactions with lichens, making reference to the broader literature on interfungal interactions (Jeffries & Young 1994) where appropriate, and suggesting some research questions that can be addressed in this area.

Saprotrophic interactions.—Recent studies (Girlanda et al. 1997; Petrini et al. 1990) show that lichen thalli commonly harbor a diverse mycoflora, but most of these fungal associates appear to be opportunistic plant- and soil-inhabiting saprotrophs that probably never form stable symbiotic associations with lichens. When lichen thalli are damaged, these saprotrophs are able to grow and degrade tissues, in part because they can manufacture a variety of generalized cell wall-degrading polysaccharidases. However, their interactions with lichens are relatively loose and ephemeral.

A number of lichen-associated fungi appear to derive their fixed carbon specifically from decaying lichen tissues. Examples mentioned by Hawksworth (1982*c*) include *Conidiobolus lichenicola*, *Endophragmiella hughesii*, *Monodictys anaptychiae*, and *Niesslia cladoniicola*. In addition, the anamorphs of many species of ascomycetes frequently develop saprotrophically over lichen thalli without forming stable relationships with them; however, they are usually not considered to be lichenicolous fungi. According to Christiansen (1980) *Lichenoconium erodens* is a virulent parasite, but one of us (P.D.) believes that it typically invades dead hosts after they have been killed by another parasite or some other reason. This has not been documented, however, and we suggest it as a research topic.

It remains to be demonstrated just how widespread the saprotrophic niche is for lichenicolous fungi. Hawksworth (1982*c*) mentioned that they appear to be less diverse than parasitic forms; he suggested also that many are probably not obligately lichenicolous saprotrophs. This would suggest that saprotrophy is a rarely derived condition within fungal groups containing lichen-associated forms. There is still considerable debate about the primitive condition of mycoparasites in the literature (Jeffries & Young 1994). If obligate parasitism is a fundamental attribute of primitive groups and saprotrophs arose from these primitive groups, phylogenetic investigations that target these fungi will prove very useful in elucidating these relationships. They may also shed light on broader evolutionary questions concerning the significance of the parasitic habit in the fungi.

To encourage investigation of obligate lichen saprotrophs we offer the following hypotheses for testing:

1) Obligate lichen saprotrophs that specialize on a single lichen species or genus will prove to be very rare in nature; most saprotrophs on lichens will be generalized facultative saprotrophs.

2) Phylogenetic analyses of groups containing obligate lichen saptrotrophs will frequently indicate a derived position for taxa that exhibit this character.

Biotrophic vs. necrotrophic interactions.—Lichen-associated fungi that obtain at least a portion of their fixed carbon from either the lichen mycobiont or photobiont should perhaps be considered parasites by definition, even if there is no apparent harm to the lichen. During the past 30 years, however, most people working on lichenicolous fungi have used the term ‘parasite’ only for a fungus that damages its host. In the literature on lichenicolous fungi, therefore, the extent to which the interaction causes damage appears to matter in the application of terms.

A standard terminology based on the aggressiveness or virulence of mycoparasites is used to describe interfungal parasite associations (Jeffries & Young 1994). Necrotrophic mycoparasites have a high virulence, are obviously destructive, and kill their hosts as a result of their activity. They tend to be generalized in their host preference and opportunistic, sometimes functioning as saprotrophs as well as parasites. In contrast, biotrophic mycoparasites exhibit a low virulence, maintain their hosts for extended periods of time, and may not show obvious signs of their presence. These parasites tend to be unusually host-specific and develop specialized infection structures or compounds.

Although very little is known about the actual basis for lichen parasite virulence, there are obvious differences in the level of damage caused by these

TABLE 1. A classification of virulence types observed in parasitic lichenicolous fungi (modified from Hawksworth, 1982*c*).

Virulence type	Host-specificity	Ecological amplitude	Phylogenetic diversity	Outward appearance	Examples
Pathogens	Generalized	Wide	Rare	Obvious and extensive damage	*Athelia arachnoidea*
Restricted discolorations	Very restricted	Narrow	Diverse	Isolated necrotic patches	*Pronectria tincta, Lichenoconium echinosporum*
Galls	Very restricted	Narrow	Diverse	Malformed thallus outgrowths	*Bachmanniomyces uncialicola, Plectocarpon lichenum*
Commensals	Very restricted	Narrow	Diverse	Little or no thallus damage	*Endococcus* spp., *Muellerella* spp., *Skyttea* spp.

fungi. Hawksworth (1982*c*) proposed a useful classification of virulence types in lichenicolous fungi (Table 1) based on these differences. He noted that only a few necrotrophic lichen parasites are known, but these are usually very obvious to collectors and are therefore most familiar. The commonest lichenicolous fungi seem to be biotrophic, restricted to one or a few hosts, and rarely kill entire lichen thalli, indicating a lengthy coevolution of these associations.

The following hypotheses relate to these presumed relationships between virulence, host range, and phylogenetic diversity:

1) Necrotrophic lichen parasites will exhibit broad host amplitudes when found in lichen communities; however, measures of their importance in communities will vary considerably over time.

2) Biotrophic parasites will be rare and more host-specific when found in lichen communities; however, they will tend to persist indefinitely at the same importance values in the community over time.

Gall-forming lichenicolous fungi.—Lichen galls (also called lichen cecidia) have been observed and studied by biologists for many years, beginning most significantly with Bachmann, who studied them anatomically, and later with Grummann (1960), who brought together all available information about lichen galls. These thallus deformations develop predictably into a morphologically distinct structure that is sometimes identical in color to the lichen or sometimes differently colored. They can be caused by a variety of infecting organisms, including numerous mites and nematodes (zoocecidia). Obligate lichenicolous fungi also frequently induce formation of galls or mycocecidia on lichens (Diederich 1996; Hawksworth 1982*c*); Martin Grube (Grube & de los Ríos 2001) estimates that there are approximately 80 known species of these unique gall-forming fungi.

Anatomical investigations of galls formed by lichenicolous fungi are few, but it is clear from these studies that gall formation by lichenicolous fungi is intricate and varied. Just as with galls formed on higher plants, lichen galls are frequently made up of lichen tissues (both mycobiont and photobiont) and mycelium of the parasite. They are considered to be among the more tightly regulated and balanced of the interactions involving lichenicolous fungi (Rambold & Triebel 1992) Given the complex morphogenetic interactions between lichen mycobionts and photobionts, it should not be surprising that similar complex interactions involving secondary fungi frequently take place (Moreau 1956). The regulation of the development of defined and predictable structures is still largely unknown. It can apparently involve direct contact with lichen mycobionts and/or photobionts, resulting in development of gall tissues composed of various combinations of lichen and parasite cells. This development involves a variety of growth-inducing and cell-degrading agents (Grube & de los Ríos 2001), some even able to control gall development at a distance, indicating a chemical control over gall morphogenesis (Bachmann 1920, 1927*a,b*).

Gall morphogenesis has been explored directly by studying the anatomy of gall-formation that documents patterns of development and the types of interactions that take place over time. It can also be studied experimentally by axenically culturing gall-forming lichenicolous fungi on resynthesized lichens in the laboratory, approaches that have not yet been taken. As more of these investigations are carried out, some of the following questions can be addressed:

1) If compounds can definitely be shown to regulate gall formation, what compounds are involved in this? How to they control morphogenesis?

2) To what extent is developmental control targeting only lichen mycobionts or photobionts? To

what extent does gall development depend on an integrated lichenized thallus?

3) How does a cecidogenous (gall-forming) habit evolve? Are cecidogenous species more or less virulent than their non-cecidogenous relatives?

4) What are the consequences of gall-formation to lichens? Are diseased lichens killed? Is there a pattern indicating evolution of virulence in groups of lichenicolous fungi containing gall-forming species?

Lichenicolous lichens.—Unlike other mycoparasitic associations, lichen-associated fungi are commonly lichen mycobionts in search of a photobiont. Indeed, the vast majority of ascomycete lichenicolous fungi are assumed to be lichenicolous lichens since they appear to live directly on photosynthate produced by lichen photobionts (Rambold & Triebel 1992). These organisms may begin growth as a free-living mycobiont attached to a host lichen, using the photobiont of the host as a source of fixed carbon, and then later become an independent lichenized thallus. A good example is the lichen *Diploschistes muscorum*, the mycobiont of which initially parasitizes squamules of *Cladonia* species and forms an association with the host photobiont. Over time, *D. muscorum* acquires its own unique photobiont and becomes independent (Friedl 1987). This exchange of photobionts appears to be necessary for the establishment of independent thalli of *D. muscorum*, but the causative mechanism is not known. Another example is the parasitic lichen *Fulgensia bracteata*, which begins development as germinating ascospores on the thallus of another lichen, *Toninia sedifolia*. In this case, however, the parasitic lichen retains the photobiont of the host during its development (Ott et al. 1995). This behavior is similar to that of germinating mycobionts that are able to acquire photobiont cells from the soredia of other lichens (Ott 1987*a,b*).

There are also cases of lichenized thalli colonizing and growing on other lichenized thalli, causing varying degrees of damage to the host. These interactions are obviously parasitic, but the nutritional behavior of the fungus is still very much that of a lichen mycobiont. The host lichen serves either as a source of photobiont cells or as a substratum. The many examples of lichenicolous lichens already described in the literature suggest that it is a common strategy in many groups of lichens (Hawksworth 1982*c*; Poelt & Dopplebaur 1956; Rambold & Triebel 1992). The variety of these interactions indicates enormous flexibility in the way these fungi form symbiotic associations. If it is true that most ascomycete lichenicolous fungi are nutritionally lichen mycobionts, there are a number of interesting questions that can be asked:

1) Do obligate lichen-formers and facultative lichen-forming lichenicolous lichens differ nutritionally?

2) Do obligate and facultative lichen-forming fungi differ in symbiont specificity?

3) How are lichens and lichenicolous lichens related phylogenetically?

Host specificity.—The host specificity of described lichenicolous fungi appears to be high (Diederich 2000), with as many as 95% thought to be associated with only a single lichen genus. The number of definitely non-specialized species is extremely low (Table 2), although the accuracy of this impression is difficult to assess objectively. Nevertheless, since collectors of lichenicolous fungi generally examine hundreds or thousands of thalli of almost all lichen species present, they usually know much about the host range of the fungus for a given locality.

Table 2 includes less than 25 species, which represents around 2% of the known species of lichenicolous fungi. Most other presumed non-specialized species, such as *Muellerella* spp., *Endococcus* spp. and many others appear to be heterogeneous assemblages of several species. As more lichenicolous fungi are discovered, we expect most to be specialized, which means that the specialized ones might well be around 99% of all lichenicolous fungi.

If the 95% figure for host-specificity is true, the specificity of lichenicolous fungi is extreme even for the most speciose and host-specific parasites. In a broad review of host-parasite interactions, Price (1980) found that host-specificity varies considerably among parasitic groups of organisms, but no group has a level approaching 95%. The most host-specific groups are generally composed of species that form the most intimate relationships with hosts. The evolutionary explanation for this has always been that coevolution between a parasite and its host favors characteristics in each that lead to unusually specific and integrated interactions between the two. Given the apparently high level of host specificity in lichenicolous fungi, we would expect the same explanation to apply. However, the actual host specificity of most lichenicolous fungi is not known with certainty.

It appears that some lichen groups harbor more host-specific lichenicolous fungi than others. For example, Hawskworth (1982*d*) discovered that some lichen groups (Arthopyreniaceae, Thelotremataceae) harbor few obligate lichenicolous fungi, some (Cladoniaceae, Pertusariaceae) harbor a moderate number, and one group (Peltigeraceae) harbors an unusually high number of these fungi. Similar genera, such as *Lobaria*, *Sticta*, and *Pseudocyphellaria*, are as rich in lichenicolous fungi as *Peltigera*, the only difference being that these gen-

TABLE 2. Examples of well-documented, apparently non-specialized species of lichenicolous fungi.

Taxonomic group	Lichenicolous fungus	Hosts
Dothideales	*Lichenostigma maureri*	Fruticose epiphytic lichens (*Alectoria, Evernia, Letharia, Pseudocyphellaria, Usnea,* etc.)
Hypocreales	*Acremonium* spp.	Thalli of diverse lichen species
	Nectriopsis lecanodes	*Lobaria, Nephroma, Parmeliella, Peltigera, Pseudocyphellaria,* etc.
	Nectriopsis parmeliae	*Parmelia s.l.*
	Paranectria oropensis	Corticolous lichens (*Buellia, Degelia, Lepraria, Pannaria, Physconia,* etc.)
	Trichonectria hirta	Crustose epiphytic lichens
	Trichonectria rubefaciens	*Parmelia s.l.*
Lecanorales	Some species of *Phacopsis*	*Parmelia s.l.*
Sclerotial basidiomycetes	*Athelia arachnoidea*	Epiphytic lichens and other cryptogams
	Leucogyrophana lichenicola	*Cladonia* subgen. *Cladina, Stereocaulon*
	Marchandiomyces corallinus	*Cladonia, Lasallia, Lecanora, Lepraria, Parmelia s.l.,* etc.
Anamorphic ascomycetes	*Cornutispora ciliata* and *C. lichenicola*	Diverse lichen species
	Illosporiopsis christiansenii	Corticolous lichens (*Parmelia s.l., Physcia,* etc.)
	Lichenoconium erodens	Dead lichens
	Lichenoconium lecanorae	Lecanora, *Parmelia s.1.,* etc.
	Phaeosporobolus usneae	Fruticose and rarely crustose thalli of epiphytic lichens

era are rarer in Europe and best represented in other parts of the world, where lichenicolous fungi were unexplored until very recently. For example, Etayo and Diederich (1996) recorded 21 species of lichenicolous fungi on *Lobaria pulmonaria* in the western Pyrenees, which indicates that the real number of parasites on *Lobaria* must be much higher.

Differences in the numbers of lichenicolous fungi among lichen groups may be caused by a number of factors, many discussed by Hawksworth (1982*d*):

1) Habitat, nutritional, and chemical differences among lichen hosts. The members of the Peltigerales may be more suitable substrates to a wider variety of fungal colonizers for chemical (types and amounts of secondary metabolites) and nutritional (higher nitrogen content) reasons. Etayo and Diederich (1996*b*) added that these lichens with very large thalli are often decaying in older parts and often grow in humid conditions, which would make them an appropriate ecological niche for many lichenicolous fungi.

2) Wide geographic distributions. Gregory (1990) found in a review of the vertebrate parasite-host literature that host species with large geographic ranges harbor a greater number of parasite species than those with smaller ranges. Do widely distributed lichens harbor more parasites than narrowly distributed ones? This would appear not to be true for lichenicolous fungi. For example, the genus *Pseudocyphellaria* (if we exclude a few common, cosmopolitan species) has a much more restricted area of distribution than *Peltigera,* but seems to be equally infected by parasites; also, species of *Menegazzia* in Papua New Guinea are nearly all endemics, but nevertheless have many parasites; *Thamnolia* is restricted to polar and alpine regions, but nevertheless has many parasites.

3) Availability over evolutionary time. The most ancient groups of organisms should harbor the most parasites since they would have been available for colonization longer (Hawksworth 1982*d*). Is this true for ancient groups of lichens?

If coevolution is driving host specificity of these associations, lichen groups with the most parasites should also be the most speciose, with each parasite adapted to its own parasite, and this is not always the case. Many species in the genus *Peltigera,* for example, harbor dozens of different lichenicolous fungi. The high diversity of associations on certain lichens must be caused not by species-specific coevolution but by the independent adaptation of many unrelated lichenicolous fungi to the same lichen host. Given our ability now to reconstruct phylogenies of lichens known to harbor lichenicolous fungi, the evolutionary development of these associations can be investigated more rigorously.

The following hypotheses relate to the origin and ecological consequences of host-specificity in lichenicolous fungi:

1) Host specificity of lichen parasites will be negatively correlated with parasite virulence. However, the most generalized and virulent parasites are not common or diverse in most lichen communities.

2) Groups of lichens harboring the greatest diversity of obligate lichenicolous fungi will exhibit one of the following two characteristics:

a.–The lichen group will itself be diverse, with many lichen species harboring well adapted lichen parasites (coevolutionary origin). For example, in *Lobaria*, some species harbor a distinct *Plectocarpon* species; however, these *Lobaria* species, like *L. pulmonaria*, frequently harbor many other well-adapted parasites as well. b.–Most lichens in the group will harbor a wide assortment of unrelated parasites (independent adaptation).

Microscopic and ultrastructural investigation of interactions.—Several investigators have observed the zones of contact between lichenicolous fungi and lichens microscopically. Generally, these have been studies of lichenicolous ascomycetes that derive their nutrition from lichen photobiont cells. These interactions frequently involve haustorial connections between the fungus and the lichen photobiont cells, an observation that suggests a mode of nutrition similar to that of the lichen host (citations in Rambold & Triebel 1992). There are also lichenicolous fungi that are either algal parasites, attacking and killing the photobiont of the lichen host (e.g., *Zwackhiomyces coepulonus* on *Xanthoria elegans*, studied by Grube & Hafellner 1990) or mycoparasites that form direct haustorial connections with the lichen mycobiont (de los Ríos & Grube 2000; de los Ríos et al. 2000; Diederich 1996). Sometimes a preference is difficult to establish because the parasite can attack either lichen partner, although one is usually attacked first. For example in the Dacampiaceae, which includes both lichen-forming and lichenicolous species, the lichenicolous species are apparently necrotrophic mycoparasites that form penetrating haustorial connections with mycobiont hyphae, ultimately causing destruction of tissues; photobiont cells can be penetrated, but only in advanced stages of infection (de los Ríos & Grube 2000).

In the gall-forming heterobasidiomycete *Biatoropsis usnearum*, which grows on *Usnea* species, the parasite forms unique tremelloid haustorial connections with the host fungus and is therefore definitely a mycoparasite (Diederich 1996). Grube and de los Ríos (2001) were able to visualize these interactions using toluidine blue and acridine orange as selective stains for hyphae of *B. usnearum*. They found that gall development resulted in loss of algal cells, formation of basidia (Diederich & Christiansen 1994), and an organized transformation of host hyphae. It is interesting that in *B. usnearum*, the galls appear to contain no usnic acid or any other lichen compounds, suggesting that their production by the lichen mycobiont is somehow suppressed. At maturity, the galls have a central zone of closely packed host hyphae and a basal zone of host hyphae resembling the central cord of *Usnea* oriented horizontally. These observations suggest some sort of regulation of normal host development during gall formation. However, the interaction is decidedly negative for the lichen since mycobiont hyphae are steadily penetrated by the parasite as the galls develop until most are dead. The galls of other lichenicolous heterobasidiomycetes are similar in appearance to *B. usnearum*.

Ultrastructural studies of interfungal associations (reviewed in Jeffries & Young 1994) show that there may or may not be an actual physical zone of interaction between a fungal parasite and its fungal host. Some necrotrophic fungi kill other fungi at a distance through the production of toxic compounds. When there is physical contact of the parasite and host, the contact my involve no cellular penetration at all, penetration followed by production of specialized absorptive structures (haustoria), even complete cytoplasmic fusion of the parasite and host hyphae. The consequences of these interactions vary from rapid destruction of the host (necrotrophy) to the formation of stable symbiotic associations (biotrophy). The host can display various reactions to the presence of the parasite, including various anomalous wall thickenings at the site of penetration. Such host responses are sometimes also seen in lichens attacked by lichen parasites (e.g., Glenn et al. 1997).

It is assumed that these zones of contact represent sites for nutrient exchange between the parasite and host, although such exchanges are rarely measured directly. It is also assumed that wall-degrading enzymes are necessary for penetration of the fungal host. However, there is little or no evidence to support these assumptions. It is also assumed that the evolution of a lichenicolous habit involves the acquisition of structures, compounds, or behaviours that permit the effective use of lichens as hosts. However, there are presently no phylogenetic studies that can shed light on this.

Since so little is presently known about infection zones of lichenicolous fungi, few generalizations can be made as yet about how various sorts of interactions relate to virulence, host specificity, geographic range, or phylogenetic position. To stimulate this effort, we offer the following hypotheses for testing:

1) Highly stable and specialized biotrophic interactions will exhibit modes of nutrient acquisition involving only one lichen biont and little host damage.

2) Especially virulent necrotrophs will produce generalized toxins or penetration structures that damage both the mycobiont and photobiont of a wide variety of lichens.

3) In natural groups of ascomycetes that contain lichenicolous and lichen-forming members, lichenicolous members will always prove to be derived from lichen-formers (Lutzoni et al. 2001).

Axenic culture and culture requirements of lichenicolous fungi.—Experimental approaches to the study of lichenicolous fungi depend heavily on the isolation and maintenance of axenic cultures of these fungi. Dozens of species have been isolated to date, and these have been used in a number of studies of lichen-parasite interactions. Methods used to isolate lichenicolous fungi are similar to those used for microfungi generally (Lawrey 2002), and many can be brought into culture easily. However, there are groups of lichenicolous fungi that appear to be especially difficult to culture and it would be interesting to investigate the reasons for these difficulties. For example, some gall-forming lichenicolous fungi (*Epicladonia* spp., *Bachmanniomyces uncialicola*) are difficult to isolate in culture, possibly because of the strict growth requirements of these fungi.

Taxonomic investigations of lichenicolous fungi seldom include isolation and culture, although Lowen and Hawksworth (1986) mentioned a number of studies in which fungi were isolated and characterized in culture. This is especially useful in documenting anamorph-teleomorph relationships since single-ascospore isolates sometimes produce conidia in culture. For example, Lowen and Hawksworth (1986) obtained single ascospore isolates of the lichenicolous pyrenomycete *Pronectria santessonii* and observed production of *Acremonium* conidia in the cultures. Establishing anamorph-teleomorph connections no longer depends so heavily on isolating cultures since molecular techniques can accomplish this also. Nevertheless, the isolation and deposit of these fungi in culture collections makes them available to all investigators and provides numerous opportunities for experimental work.

Based on the limited information available, isolation of most lichenicolous fungi is unusually challenging. A recent paper by Crittenden et al. (1995) provided a good indication of this. They attempted isolation of a wide assortment (1,183 species) of lichen-forming and lichenicolous fungi from 20 countries and found that lichenicolous fungi were particularly difficult to isolate. Only 31% of these species were successfully isolated, compared with 42% of the lichen-forming fungi. The authors suggested that the unusual nutritional requirements of these fungi limit successful isolation. Nevertheless, this study demonstrates that many lichenicolous fungi can be isolated if attempts are made to do so. If fungi are successfully isolated, it is essential that cultures be placed in one of several available culture collections so that other investigators may also obtain them. Examples of appropriate collections are given in Lawrey (2002).

Once isolates of lichenicolous fungi are obtained, laboratory experiments can be done on a variety of topics. For example, the basic nutritional requirements are largely unknown for nearly all of these fungi. Standard fungal growth media are used to maintain most lichenicolous fungi in culture, but it is likely that optimal growth depends on culture conditions unique to each species or group and such information can be obtained only by thorough laboratory experiment. For example, Gilbert (1988) reported laboratory studies of *Athelia arachnoidea* isolated by M. McQuilken and maintained on malt agar. This fungus apparently grows over a wide range of temperatures (from 0° to nearly 30°C) in culture, with an optimum at 20°C. As another example, consider the growth in culture of the lichenicolous basidiomycete *Marchandiomyces corallinus*, which can be collected from a variety of lichens in North America and Europe and easily isolated. In standard mixtures of Sabouraud's-dextose medium, the fungus grows slowly and can be maintained indefinitely. However, if a low-protein mixture is used (1/10 of the normal amount of neopeptone, a complex enzymatic protein digest), a significantly accelerated growth is observed (Fig. 2). Such a preference may be adaptive for mycoparasites that colonize living lichens since these tissues generally have a higher-than-normal carbohydrate content and C:N ratio. A similar preference for lichen tissues has been observed for an undescribed lichenicolous *Fusarium* sp. that degrades lecanoric acid (Lawrey et al. 1999). This fungus will grow on PDA in the laboratory, but will only form conidia when supplied with lichen tissues containing secondary compounds (Lawrey, unpublished). Obligate lichenicolous fungi are likely to have many unusual and specific chemical requirements, and these can be investigated most effectively using isolated cultures.

Given the lack of much information about the isolation and culture of lichenicolous fungi, we offer the following hypotheses to stimulate discussion and encourage investigation:

1) The ease of isolation and culture of lichenicolous fungi will depend on the host-specificity of the fungus and the nature of the association. The easiest to culture will be saprotrophs, followed by generalized necrotrophs and biotrophs; the most recalcitrant will be biotrophs, which make up most of the lichenicolous fungi.

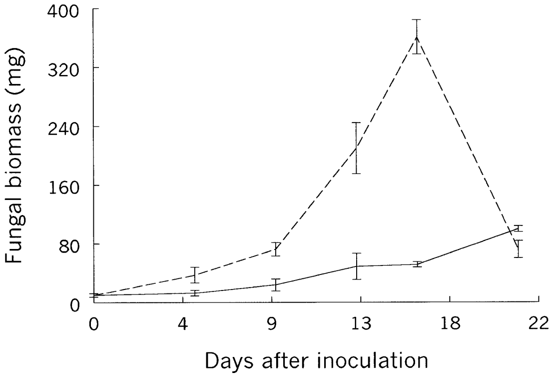

FIGURE 2. Growth (measured as dry biomass increase, mg) of *Marchandiomyces corallinus* mycelium grown in Sabouraud's-dextose medium for 30 days. Solid line indicates growth on complete standard medium; dashed line indicates growth on Sabouraud's made with 1/10 the normal amount of neopeptone.

2) Successful isolation and growth of strict biotrophs will depend on mimicking the nutritional conditions provided by the lichen host.

3) Gall-forming lichenicolous fungi will prove to be the most difficult of lichenicolous fungi to culture in the laboratory. This may require either *in vivo* culturing of galls or axenic resynthesis of the associated lichen mycobionts and photobionts along with the gall-forming fungus. However, such an approach will demonstrate the presumed complex morphogenetic interactions among the associates.

Chemical interactions—mycoparasite enzymes and inhibitory effects of lichen compounds.—The ability of a lichenicolous fungus to use a given lichen thallus (either living or dead) as a source of fixed carbon depends on a number of measurable chemical characteristics of both the lichen host/substrate and the lichen parasite/saprobe. The elucidation of these chemical interactions may help to explain many of the unusual characteristics of these associations (host specificity, phylogenetic diversity, etc.).

The well-known antibiotic properties of lichen secondary metabolites would appear to limit the colonization of lichen thalli by all but the most tolerant fungi. Hawksworth (1982*c*) mentioned that opportunistic fungal saprotrophs (e.g., species of *Aspergillus*, *Penicillium*, *Trichoderma*) rarely grow on lichens containing secondary compounds, even though it is obvious from several studies (Girlanda et al. 1997; Petrini et al. 1990) that these fungi can be isolated from lichen thalli and are therefore common enough in most lichen habitats. There is also abundant data from clinical tests that lichen compounds are effective as antifungal and antibacterial agents (Yamamoto et al. 1993).

If lichen compounds are generally inhibitory to fungi, however, lichenicolous fungi must be tolerant of at least certain of these compounds. There is some evidence to support this hypothesis: i) A number of unrelated lichenicolous fungi exhibit better growth on lichen tissues containing lichen compounds than on tissues with the compounds removed (Lawrey 1997); ii) Some lichenicolous fungi are intolerant of most lichen compounds, but tolerate the specific compounds of preferred lichen hosts (Lawrey et al. 1999); and iii) Some lichenicolous fungi colonize certain lichens only when the compounds of these lichens are removed (in laboratory experiments) or degraded by other fungi (in the habitat). For example, the familiar hypocrealean ascomycete *Nectriopsis parmeliae* is commonly collected from a variety of lichen species in North America, but will grow on tissues of certain of these lichens only if compounds are removed. Compounds of the lichen *Punctelia rudecta* (especially lecanoric acid) inhibit growth of *N. parmeliae* in the laboratory. In this case, the presence of *N. parmeliae* on *P. rudecta* appears to be due to presence of another lichen parasite, a *Fusarium* sp. that is able to degrade lecanoric acid and other inhibitory compounds of *P. rudecta*. Further evidence for this hypothesis is the almost complete co-occurrence of *N. parmeliae* with the *Fusarium* pathogen in the community (Lawrey 2000).

It is perhaps unwise to generalize too much from these results, but they indicate that lichenicolous fungi make host preferences based in part on chemistry. They also emphasize the complex interplay among lichens and lichen-associated fungi in communities. The extent to which chemistry regulates these associations is extremely variable, and the chemical interactions involved in any specific association must be worked out experimentally.

How do lichen compounds actually limit the use of lichens by mycoparasites? There are a number of different ways this can happen. Firstly, spores or other propagules must in many cases be able to germinate in or on a lichen thallus, and lichen compounds are known to inhibit fungal spore germination (Pyatt 1973; Vartia 1973; Whiton & Lawrey 1982). For lichenicolous fungi that make spores, conidia or other air-borne propagules, simple spore germination tests can be done to establish the requirements for germination and the extent to which lichen thallus chemistry influences germination.

Once it begins growth, a fungal colonist must somehow acquire carbon from the lichen, either in the same way as the mycobiont (direct transfer of photosynthate from the photobiont) or by producing cell wall-degrading enzymes to penetrate mycobiont or photobiont cells. Hawksworth (1982*c*) suggested that many lichenicolous fungi are actually mycobionts; however, for most lichenicolous fungi the mode of nutrition is still very much an open question.

For a lichen parasite, acquisition of carbon from the lichen host depends in part on its ability to produce appropriate cell wall-degrading enzymes. In many cases, especially for generalized saprotrophs/necrotrophs, the enzymes will be similar for lichen-associated fungi as for related non-lichenicolous fungi. For example, Thorn et al. (1998) characterized the polysaccharidases of the sclerotial basidiomycete *Leucogyrophana lichenicola*, isolated from *Cladonia* mats in Ontario. They found no differences in the enzymes of this lichenicolous species and various non-lichenicolous wood-rotting relatives, suggesting that the fungus may utilize substrates other than lichens. For more specialized biotrophic lichenicolous fungi, we can hypothesize that lichenicolous fungi are in many cases uniquely adapted to exploit lichens, either by the kinds of enzymes they produce or by their ability to tolerate specific lichen compounds.

Only a few studies have been published on enzyme activity in lichen mycoparasites, and these considered only generalized saprotrophs or necrotrophs. Still, there is clear evidence that lichen compounds can regulate production and activity of the enzymes produced by lichen-associated fungi.

1) The generalized necrotroph *Nectriopsis parmeliae* produces a variety of polysaccharidases whose overall catalytic activity depends on the chemistry of the lichen tissues provided as a substrate (Torzilli & Lawrey 1995). On tissues of the lichen *Flavoparmelia baltimorensis*, which commonly harbors *N. parmeliae*, enzyme activity is high regardless of the presence of acetone-soluble lichen compounds. On tissues of *Lasallia papulosa*, which do not support growth of this fungus in the lab, enzyme activity is high only if secondary compounds (especially lecanoric acid) are first removed. These results suggest that the host ecology of *N. parmeliae* is constrained by the antibiotic effect of certain lichen compounds on its particular suite of polysaccharidases.

2) The generalized necrotroph *Marchandiomyces corallinus* is observed commonly on the lichen *Flavoparmelia baltimorensis*, but only rarely on *Lasallia papulosa*, and it will not grow on tissues of *L. papulosa* in the laboratory unless compounds (especially lecanoric acid) are extracted with acetone (Lawrey et al. 1999). However, lecanoric acid does not inhibit the polysaccharidases of *M. corallinus* (Torzilli et al. 1999), which indicates that the chemical inhibition of *M. corallinus* by *L. papulosa* involves a general inhibition of growth, not of enzyme activity.

3) The virulent lichen pathogen *Fusarium* sp. (NRRL 26803) grows on a wide variety of lichens in the eastern United States. In the laboratory, it will grow on lichen tissues regardless of the presence of secondary compounds. It produces enzymes that degrade not only lichen cell walls but also lichen compounds (e.g., degradation of lecanoric acid in *Punctelia rudecta* over a 90-day period, Fig. 3). This ability to degrade lichen compounds is apparently unusual in the clade containing this *Fusarium* sp. since known related species, all of which are entomogenous in habit, fail to produce the necessary enzymes (Torzilli et al. 2002).

These few studies illustrate the fact that the enzymes produced by generalist necrotrophic lichen parasites help to define their ecology and host preferences. To the extent that the type and diversity of their enzymes uniquely adapt fungi to a lichenicolous habit, the study of these enzymes will also shed light on the biochemical changes that can lead to the evolution of a lichenicolous habit.

We are not aware of any enzyme studies done on host-specific biotrophic lichen parasites, although it is likely that the most interesting enzymes will be found in these fungi. However, the difficulties in isolating these fungi and maintaining them in culture make the study of their enzymes equally difficult.

In this section, our intent was to demonstrate the range and diversity of potential chemical interactions among lichens and lichen-associated fungi. Since every association is unique, each will undoubtedly involve its own set of chemical regulators. Elucidating the details of these interactions will present unusual challenges to investigators. In an attempt to provide a broad theoretical framework for researchers, we offer some general hypotheses for testing:

1) Lichen compounds are most inhibitory to common, generalized, and opportunistic fungal colonists not uniquely adapted to lichens.

2) Lichenicolous fungi will generally be more tolerant of secondary metabolites than non-lichenicolous fungi.

3) The most specialized lichenicolous fungi will be most tolerant of lichen compounds produced by their hosts.

4) The diversity of cell wall-degrading polysaccharidases will be greatest in generalized necrotrophs and lowest in host-specific biotrophs.

5) Enzymes of the most specialized biotrophic lichen parasites will have narrow ranges of activities and will be uniquely adapted to the chemistry of their hosts.

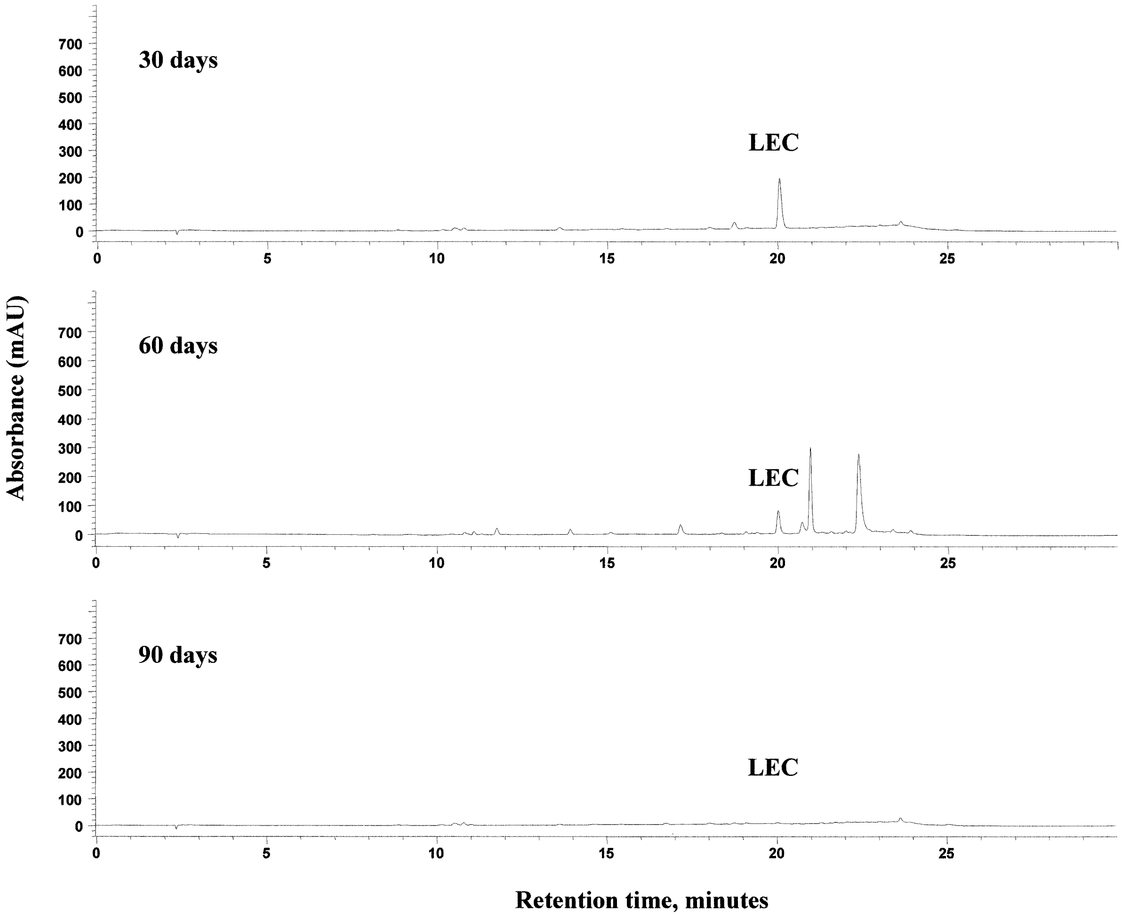

FIGURE 3. HPLC chromatographs of extracts of the lichen *Punctelia rudecta* exposed to *Fusarium* sp. (NRRL 26803) to 30 (top), 60 (middle), or 90 days (bottom). The position of the lecanoric acid (LEC) peak is shown. Other peaks are *Fusarium* products in the culture filtrate. Absorbance units (mAU = milli-absorbance units) represent the absorbance by the detector at 254 nm. Modified from Lawrey (2000).

THE DIVERSITY OF LICHENICOLOUS FUNGI

Lichenicolous ascomycetes.—The great majority (over 95%) of presently described lichenicolous fungi belong to the ascomycetes. Their ascomata are either apothecia or perithecia, which are typically small, mostly between 0.1 and 0.4 mm in diam., and long-lived. They are therefore easily able to be present on host thalli for periods of many months or years. In several very specialized species, like *Arthonia intexta*, the ascomata are reduced or even entirely absent, and the asci develop intrahymenially within the ascomata of their host (Hertel 1969). In *Lichenostigma elongata*, no actual well-delimited ascomata are visible, and the fertile hymenia develop within swollen stromatic structures formed by the fungal mycelium (Navarro-Rosinés & Hafellner 1996). Many lichenicolous ascomycetes have the ability to produce vegetative mitospores, either enclosed within pycnidia (these fungi are usually called coelomycetes) or not (called hyphomycetes). The function of these mitospores is not entirely known, but it is supposed that they are in most cases conidia, that is vegetative spores permitting asexual reproduction, especially when they are large, septate, pigmented, or ornamented. In some cases, however, small, hyaline, smooth-walled, aseptate mitospores may represent spermatia of the fungus. This has never been documented experimentally and would be a worthy subject for research.

Mitospores are entirely unknown in many species or genera of lichenicolous fungi, like *Odontotrema* (Diederich et al. 2002) or *Skyttea* (Diederich & Etayo 2000). In other taxa, like *Abrothallus* species, pycnidia with characteristic conidia are frequently present together with the ascomata. In *Trichonectria hirta*, the reddish perithecia are short-lived, but the whitish hyphomycetous anamorph referred to the genus *Cylindrocarpon* is present over longer periods and betrays the presence of the fungus even when sterile (Diederich 1989). In species of *Hemigrapha*, pycnothyrial conidiomata are macroscopically indistinguishable from thyriothecioid ascomata, and it has been suggested that the same fruiting body can serve as conidioma and ascoma (Diederich & Wedin 2000). In many known examples, ascomata of a lichenicolous fungus are regularly found growing together with pycnidia, but it is not clear if both belong to the same fungus. For example, the stromatic conidiomata of *Phaeosporobolus* species are frequently found beside the morphologically and anatomically similar stromatic ascomata of *Lichenostigma* species, and there was speculation that they might be the same fungus (Alstrup & Hawksworth 1990). However, the discovery of the genuine teleomorph of *Phaeosporobolus* by Alstrup and Hawksworth (1990), eventually described as the new genus *Diederimyces* (Etayo 1995*b*), proved that this resemblance does not reflect any phylogenetic relationship.

For a large number of species and even genera of lichenicolous fungi, only the anamorph is known, and all attempts to associate them with any known teleomorph have so far failed. These include very common, widespread, and well-known genera like the coelomycetous *Lichenoconium*, *Lichenodiplis*, and *Vouauxiella*, or the hyphomycetous *Illosporiopsis*, *Sclerococcum*, or *Taeniolella*. Indeed, the absence of a teleomorph would have once caused some doubt that these fungi are really ascomycetous, but it is now generally accepted that they are. For some of them, like *Illosporiopsis*, this has recently been confirmed by molecular studies (Sikaroodi et al. 2001). The international code of botanical nomenclature (ICBN) allows anamorphs of non-lichenized fungi to have distinct names. For example, the anamorphs of *Abrothallus* are included in the form-genus *Vouauxiomyces* (Hawksworth 1981), even if their teleomorph is known; Grube et al. (1995) recently described the new anamorphic genus *Helicobolomyces* for a lichenicolous *Arthonia*-species with peculiar, helicoid conidia. With so much recent progress in molecular taxonomy, the tendency is now to stop using two or even more names for different morphs of a single fungus, and to use anamorph names exclusively for mitosporic fungi not clearly associated to a teleomorph. Thus, instead of naming a fungus *Vouauxiomyces truncatus*, we should simply speak of the pycnidial morph of *Abrothallus microspermus*.

Lichenicolous ascomycetes belong to numerous different orders, although some orders or families are particularly rich in them. A general overview of all known genera of lichenicolous fungi is given in Table 3, together with their systematic arrangement, estimates of species numbers, and main literature references for each genus. Summary information (Table 4) indicates clearly that the overwhelming majority of lichenicolous fungi are ascomycetes (some known only as mitosporic ascomycetes at present).

Lichenicolous basidiomycetes.—Until around 15 years ago, lichenicolous basidiomycetes were considered exceptional, with only a few species known. For example, the necrotroph *Athelia arachnoidea* and the parasite *Omphalina ericetorum*, a member of the Agaricales that parasitizes *Peltigera* thalli, were mentioned in the literature. A second agaricoid species, *Fayodia leucophylla*, was also known from *Peltigera* (Alstrup & Hawksworth 1990), but the distinction between these two species was questioned by Santesson (1993). In the 1980s, Diederich (1986) and Diederich and Marson (1988) described two lichenicolous species of *Tremella*, followed by a paper by Diederich and Christiansen (1994) showing that the well-known but mysterious galls on *Usnea* often called *Biatoropsis usnearum* are basidiomata of a heterobasidiomycete. In 1996, Diederich presented a worldwide revision of the lichenicolous heterobasidiomycetes, accepting 54 species.

Practically speaking, lichenicolous basidiomycetes can be divided into three groups (Table 3), although they do not reflect phylogenetic relationships: i) lichenicolous Agaricales, with around three species of *Omphalina*/*Fayodia*; ii) a heterogeneous assortment of sclerotial fungi, including *Athelia*, *Leucogyrophana*, *Marchandiobasidium* (anamorph *Marchandiomyces*), and probably some other yet unnamed species; and iii) heterobasidiomycetes.

Lichenicolous sclerotial fungi are not host specific, although strong preferences for certain host genera have been observed. *Leucogyrophana lichenicola* is more or less confined to species of *Cladonia* and *Stereocaulon*, and typically infects the lower, sometimes dying parts of the thalli. *Marchandiomyces aurantiacus* is a virulent parasite with seasonal appearances on epiphytic macrolichens (mainly *Physcia* species), during which the host populations become strongly reduced. *Marchandiomyces corallinus* is commonly found on species of *Parmelia s.l.*, *Physcia s.l.*, *Lepraria*, *Lecanora conizaeoides*, and *Lasallia*, suggesting that several cryptic species might be involved, with each one confined to a single host. However, recent population genetic results (Molina, DePriest and Lawrey, unpublished) indicated that this is probably not true. *Marchandiomyces* species were for a long time considered as hyphomycetes, although basidiomycetous affinities were hypothesized, and Sikaroodi et al. (2001) proved by molecular methods that the genus effectively belongs to the basidio-

TABLE 3. A general overview of all known genera of lichenicolous fungi, together with their systematic arrangement. Estimates of species numbers and main literature references are provided for each genus.

	No. species[1]	References[2]
Ascomycota		
Agyriales		
Agyriaceae		
Hafellnera	0-1-0	(245)
Rimularia	0-3-0	(245)
Arthoniales		
Arthoniaceae		
Arthonia	80-0-1	(2, 7, 8, 11, 14, 15, 32, 66, 87, 91, 93, 94, 107, 108, 156, 172, 174, 184, 188, 255, 280, 287, 305) [incl. anam. *Helicobolomyces*]
Roccellaceae		
Enterographa	1-0-0	(203)
Lecanographa	3-0-0	(80)
Mazosia	1-0-0	(203)
Opegrapha	47-0-0	(9, 15, 19, 51, 57, 91, 114, 120, 179, 183, 184, 192, 203, 219, 277, 306)
Paradoxomyces	1-0-0	(203)
Perigrapha	1-0-0	(123)
Plectocarpon	15-0-0	(15, 29, 68, 162, 255, 257, 262, 286)
Incertae sedis		
Arthophacopsis	1-0-0	(125)
Chaetothyriales		
Chaetothyriaceae		
Biciliopsis	1-0-0	(15, 301)
Herpotrichiellaceae		
Capronia	9-0-0	(15, 93, 100, 147, 154, 190)
Dothideales s.l. (incl. Microthyriales, Mycosphaerellales, Patellariales, Pleosporales)		
Dacampiaceae		
Clypeococcum	7-0-0	(106, 120, 122, 140, 146, 149, 231, 239)
Dacampia	2-1-0	(147, 153, 170)
Kalaallia	1-0-0	(9, 237)
Polycoccum	38-0-0	(15, 21, 31, 43, 44, 51, 62, 91, 157, 187, 160, 164, 203, 220, 225, 283)
Pseudonitschkia	1-0-0	(56)
Pyrenidium	27-0-0	(9, 203, 306, 307)
Weddellomyces	11-0-0	(1, 9, 39, 153, 154, 221, 224)
Dimeriaceae		
Keratosphaera	4-0-0	(203)
Dothioraceae		
Plowrightia	1-0-0	(51)
Leptosphaeriaceae		
Leptosphaeria s.l.	3-0-0	(51, 147)
Ophiobolus s.l.	2-0-0	(51)
Lichenotheliaceae		
Lichenostigma	13-0-0	(40, 111, 127, 130, 184, 216, 267)
Microthyriaceae		
Lichenopeltella	23-0-0	(15, 79, 99, 135, 136, 203, 209, 253, 254, 259)
Mycosphaerellaceae		
Sphaerulina s.l.	5-0-0	(51)
Naetrocymbaceae		
Leptorhaphis	1-0-0	(184)
Parmulariaceae		
Hemigrapha	8-0-0	(82, 139, 203, 293, 294)
Patellariaceae		
Stratisporella	1-0-0	(15, 110, 194)
Tryblidaria	2-0-0	(51)

TABLE 3. Continued.

	No. species[1]	References[2]
Pleomassariaceae		
Lichenopyrenis	1-0-0	(45)
Pleosporaceae		
Leptosphaerulina	1-0-0	(147)
Pleospora	4-0-0	(51, 139, 142, 276)
Pseudoperisporiaceae		
Epibryon	4-0-0	(203, 263, 301)
Neocoleroa	3-0-0	(20, 147, 203, 247, 263)
Raciborskiomyces	1-0-0	(20, 147)
Tubeufiaceae		
Tubeufia	2-0-0	(93)
Incertae sedis		
Buelliella	7-0-0	(15, 93, 110, 114, 181)
Cercidospora	17-0-0	(6, 51, 117, 119, 131, 177, 178, 227, 277, 281, 290)
Echinothecium	3-0-0	(7, 51, 250)
Karschia	4-0-0	(9, 110, 257)
Koordersiella	3-0-0	(84, 143, 203)
Lanatosphaera	2-0-0	(203)
Myxophora	5-0-0	(301)
Rosellinula	4-0-0	(83, 115)
Sphaerellothecium	13-0-0	(7, 100, 119, 135, 250, 277, 280)
Trematosphaeriopsis	1-0-0	(128)
Wernerella	1-0-0	(229, 230)
Helotiales		
Dermateaceae		
Mollisia	1-0-0	(51)
Niptera	2-0-0	(51)
Helotiaceae		
Bryoscyphus	1-0-0	(7)
Calycina (= *Pezizella*)	3-0-0	(93, 147, 190)
Gelatinopsis	2-0-0	(103, 244, 291)
Hyaloscyphaceae		
Lachnum s.l.	1-0-0	(51)
Polydesmia	1-0-0	(176)
Incertae sedis		
Echinodiscus	1-0-0	(101)
Geltingia	1-0-0	(9)
Llimoniella	6-0-0	(69)
Phaeopyxis	4-0-0	(8, 244)
Pleoscutula	2-0-0	(93, 112)
Rhymbocarpus	9-0-0	(69)
Skyttea	20-0-0	(8, 69, 93, 296)
Skyttella	1-0-0	(167)
Spirographa	1-0-0	(266 [sub *Pleospilis*])
Unguiculariopsis	11-0-0	(9, 55 [sub *Skyttea*], 69, 99, 190, 191, 193)
Hypocreales		
Bionectriaceae		
Globonectria	1-0-0	(93)
Nectriopsis	16-0-0	(4, 12, 15, 52, 70, 93, 252, 263) [some as *Nectria*]
Paranectria	3-0-0	(51, 149, 309)
Pronectria	27-0-0	(93, 196, 309)
Trichonectria	5-0-0	(93, 263, 299, 309)
Xenonectriella	1-0-0	(309)
Clavicipitaceae		
Neobarya	4-0-0	(93)
Niessliaceae		
Niesslia	6-0-0	(93, 97, 139, 143) [incl. anam. *Monocillium*]

TABLE 3. Continued.

	No. species[1]	References[2]
Lecanorales		
Acarosporaceae		
Acarospora	0-22-0	(245)
Phacopsis	13-0-0	(116, 262, 278, 279)
Polysporina	2-1-0	(241, 245)
Thelocarpon	1-4-0	(245)
Bacidiaceae		
Bacidia	1-2-0	(245)
Squamarina	0-1-0	(245)
Tephromela	3-0-0	(243)
Caliciaceae		
Calicium	0-1-0	(51)
Cyphelium	1-1-1	(269)
Candelariaceae		
Candelariella	0-4-0	(245)
Catillariaceae		
Catillaria	2-1-0	(92, 112, 245)
Halecania	0-2-0	(206)
Toninia	7-37-0	(245, 275)
Dactylosporaceae		
Dactylospora	37-0-0	(6, 9, 10, 51, 86, 110, 114, 192, 264, 277, 308)
Fuscideaceae		
Lettauia	3-0-0	(93, 168, 303)
Hymeneliaceae		
Aspicilia	0-1-0	(245)
Lecanoraceae		
Bryonora	0-1-0	(245)
Calvitimela	0-1-0	(245)
Carbonea	11-3-0	(6, 127, 245)
Lecanora	1-11-0	(245)
Lecidella	0-5-0	(245)
Miriquidica	0-6-0	(245)
Ramboldia	0-1-0	(133)
Lecideaceae		
Cecidonia	2-0-0	(278)
Lecidea s.l.	3-11-0	(245)
Steinia	0-1-0	(245)
Micareaceae		
Micarea	1-0-0	(245)
Scutula	11-4-0	(5, 9, 51, 245, 282)
Parmeliaceae		
Protoparmelia	0-6-0	(245)
Physciaceae		
Buellia	2-16-0	(28, 33, 51, 110, 132, 245, 261)
Rinodina	1-10-0	(9, 245)
Porpidiaceae		
Bellemerea	0-1-0	(245)
Immersaria	0-2-0	(245)
Mycobilimbia s.l.	1-0-0	(245)
Poeltiaria	0-1-0	(245)
Psoraceae		
Glyphopeltis	0-1-0	(245)
Psorula	0-1-0	(245)
Rhizocarpaceae		
Epilichen	1-2-0	(109, 277)
Rhizocarpon	5-25-0	(245)

TABLE 3. Continued.

	No. species[1]	References[2]
Teloschistaceae		
Caloplaca	0-37-0	(26, 233, 236, 245, 288)
Incertae sedis		
Corticifraga	2-0-0	(168)
Corticiruptor	1-0-0	(286)
Nimisiostella	1-0-0	(34)
Lichinales		
Lichinaceae		
Lichinodium	0-1-0	(245)
Phylliscum	0-1-0	(245)
Mycocaliciales		
Mycocaliciaceae		
Chaenothecopsis	30-0-0	(51, 272, 273, 274)
Sphinctrinaceae		
Sphinctrina	6-0-0	(182, 195, 242)
Ostropales		
Odontotremataceae		
Odontotrema	15-0-0	(295)
Paralethariicola	1-0-0	(38)
Stictidaceae		
Nanostictis	5-0-0	(93, 99)
Stictis s.l.	1-0-0	(265)
Thelotremataceae		
Diploschistes	0-4-0	(200)
Phyllachorales		
Phyllachoraceae		
Lichenochora	26-0-0	(15, 42, 118, 129, 213, 214, 228, 231, 232, 250, 280, 301)
Telimena s.l.	1-0-0	(51)
Pyrenulales		
Requienellaceae		
Lacrymospora	0-0-1	(13)
Parapyrenis	1-0-0	(15)
Sordariales		
Chaetosphaeriaceae		
Melanopsamma	1-0-0	(51)
Nitschkiaceae		
Acanthonitschkea	1-0-0	(10) [= *Hystrix*]
Lasiosphaeriopsis	4-0-0	(6, 9, 85, 147, 277)
Rhagadostoma	6-0-0	(215, 218)
Rhagadostomella	1-0-0	(93)
Incertae sedis		
Globosphaeria	1-0-0	(155)
Reconditella	1-0-0	(204)
Roselliniella	15-0-0	(15, 93, 164, 204, 301)
Roselliniomyces	1-0-0	(204)
Roselliniopsis	5-0-0	(6, 202, 204)
Teratoschaeta	1-0-0	(203)
Trichosphaeriales		
Trichosphaeriaceae		
Trichosphaeria	1-0-0	(51, 147)
Verrucariales		
Adelococcaceae		
Adelococcus	3-0-0	(94, 204)
Sagediopsis	6-0-0	(9, 119, 277, 301, 313)
Verrucariaceae		
Bellemerella	3-0-0	(41, 223)
Clauzadella	1-0-0	(222)

TABLE 3. Continued.

	No. species[1]	References[2]
Diederimyces	1-0-0	(90)
Endococcus	67-0-0	(3, 6, 58, 93, 95, 120, 145, 149, 202, 258, 263, 277, 292)
Haleomyces	1-0-0	(300)
Merismatium	9-0-0	(5, 8, 173, 277)
Muellerella	10-0-0	(51, 60, 152, 277)
Norrlinia	2-0-0	(147, 190)
Phaeospora	15-0-0	(8, 11, 147, 175, 239, 263)
Placocarpus	0-1-0	(25)
Telogalla	1-0-0	(301)
Verrucaria	1-13-0	(8, 27, 207, 237, 245, 289, 301)
Incertae sedis		
Stigmidium	71-0-0	(2, 9, 11, 46, 47, 51, 88, 92, 93, 113, 120, 121, 131, 139, 203, 204, 209, 249, 250, 251, 254, 256, 277, 281, 310)
Xylariales		
Xylariaceae		
Anthostomella	1-0-0	(51)
Incertae sedis		
Arthrorhaphidaceae		
Arthrorhaphis	2-3-1	(235, 260)
Gomphillaceae		
Gyalideopsis	3-1-0	(102, 198, 199)
Melaspileaceae		
Melaspilea	8-0-0	(51, 150, 192)
Microcaliciaceae		
Microcalicium	3-0-1	(51, 148, 270)
Myxotrichaceae		
Myxotrichum	1-0-0	(143)
Obryzaceae		
Obryzum	3-0-0	(16, 301)
Protothelenellaceae		
Protothelenella	2-0-0	(205)
Strigulaceae		
Strigula	1-0-0	(93)
Xanthopyreniaceae		
Didymellopsis	4-0-0	(106)
Zwackhiomyces	19-0-1	(2, 10, 15, 106, 137, 158, 164, 189, 208, 237, 301)
Incertae sedis		
Abrothallus	20-0-0	(62, 93, 120, 154, 189, 234, 285) [incl. anam. *Vouauxiomyces*]
Gyrophthorus	3-0-0	(297, 301)
Hymenobiella	1-0-0	(277)
Hypotrachynicola	1-0-0	(93)
Neolamya	1-0-0	(185)
Pleosphaeria	1-0-0	(169)
Rhynchomeliola	1-0-0	(171)
Sarcopyrenia	6-0-0	(217, 226)
Sphaeria	1-0-0	(277)
Stegilla (= *Stegia*)	1-0-0	(51)
Stellifraga	1-0-0	(10)
Thamnogalla	1-0-0	(301)
Trichophyma	2-0-0	(203)
Anamorphic Ascomycota		
Acarosporium	1-0-0	(178)
Acremonium	4(+4)-0-1	(143, 196) [2 species are anam. of *Pronectria* and 2 of *Trichonectria*]
Ampullifera	5-0-1	(143)
Aposphaeria	1-0-0	(148)
Arborillus	1-0-0	(212)
Ascochyta	2-0-0	(9, 163)

TABLE 3. Continued.

	No. species[1]	References[2]
Asterophoma	1-0-0	(148, 271)
Bachmanniomyces	1-0-0	(148)
Berkleasmium	1-0-0	(97)
Bispora		[= *Intralichen*]
Blarneya	0-1-0	(144)
Cephalosporiopsis	1-0-0	(5)
Chalara	2-0-0	(50, 99)
Choreospora	1-0-0	(54)
Cladoniicola	1-0-0	(75)
Cladosporium	1-0-0	(61, 143)
Clauzadeomyces	1-0-0	(65)
Codonmyces	1-0-0	(35)
Coniambigua	1-0-0	(97)
Cornutispora	3-0-0	(97, 104, 148, 298, 312)
Deichmannia	1-0-0	(9)
Dendrodochium	1-0-0	(143)
Dictyophrynella	1-0-0	(143)
Dinemasporium	0-0-1	(208)
Diplolaeviopsis	1-0-0	(105)
Diplosporium	1-0-0	(143)
Endophragmiella	1-0-0	(143)
Epaphroconidia	1-0-0	(30)
Epicladonia	3-0-0	(148)
Epicoccum	0-0-1	(59)
Everniicola	1-0-0	(149)
Feltgeniomyces	4-0-0	(15, 37, 62, 94)
Fenestroconidia	1-0-0	(36)
Fusarium	1-0-0	(143)
Graphium	1-0-0	(9)
Hainesia	1-0-0	(98)
Hansfordiellopsis	3(2)-0-0	(143) [2 species are anam. of *Koordersiella*]
Hawksworthiana	1-0-0	(24, 146)
Helicobolomyces		[anam. of *Arthonia*]
Hobsonia		[see *Hobsoniopsis* and *Illosporiopsis*]
Hobsoniopsis	1-0-0	(197, 317)
Illosporium	1-0-0	(143, 317)
Illosporiopsis	1-0-0	(197, 317)
Intralichen	4-0-0	(62, 143, 159) [some as *Bispora* or *Trimmatostroma*]
Kalchbrenneriella	1-0-0	(67)
Karsteniomyces	3-0-0	(9, 23, 147, 148)
Keissleriomyces	1-0-0	(148)
Laeviomyces	4-0-0	(52, 148, 181)
Lawalreea	1-0-0	(62)
Leightoniomyces	1-0-0	(140, 143)
Libertiella	5-0-0	(97, 148, 164)
Lichenobactridium	1-0-0	(97)
Lichenoconium	13-0-0	(7, 48, 49, 60, 141, 148, 184, 191, 193)
Lichenodiplis	4-0-0	(22, 148, 161, 188)
Lichenohendersonia	3-0-0	(37)
Lichenophoma	1-0-0	(148)
Lichenopuccinia	1-0-0	(151)
Lichenostella	1-0-0	(35)
Lichenosticta	1-0-0	(148)
Macrophomina	1-0-0	(98)
Melanconium s.l.	1-0-0	(81)
Milospium	4-0-0	(16, 98, 138, 143, 263)
Minutoexcipula	4-0-0	(17, 18, 120)
Minutophoma	1-0-0	(148)
Mixtoconidium	1-0-0	(89)
Monocillium		[anam. of *Niesslia*]
Monodictys	3-0-0	(99, 138, 143)
Nigromacula	1-0-0	(93)
Nigropuncta	2-0-0	(2, 148, 166)
Patriciomyces	1-0-0	(52)
Phaeoseptoria	1-0-0	(314)

TABLE 3. Continued.

	No. species[1]	References[2]
Phoma	14-0-0	(5, 37, 60, 97, 120, 134, 147, 148, 157, 178, 201)
Phyllosticta s.l.	1-0-0	(210)
Psammina	3-0-0	(78, 143)
Pseudocercospora	1-0-0	(93, 143)
Pseudorobillarda	1-0-0	(284)
Pseudoseptoria	1-0-0	(148)
Pycnopsammina	1-0-0	(97)
Pyrenochaeta	3-0-0	(51, 62, 111)
Refractohilum	5-0-0	(140, 143, 248)
Reichlingia	0-0-1	(71)
Rhabdospora	1-0-0	(184)
Sclerococcum	13-0-0	(2, 21, 23, 62, 72, 90, 96, 97, 98, 124, 138, 143)
Sessiliospora	1-0-0	(143)
Sphaeromma		[anam. of *Keratosphaera*]
Spilodochium	1-0-0	(97)
Sporhaplus		[anam. of *Keratosphaera*]
Stromatopogon	2-0-0	(63, 74)
Stygiomyces	1-0-0	(56)
Taeniolella	16-0-1	(3, 8, 9, 52, 62, 64, 76, 77, 126, 143)
Taeniolina	0-0-1	(61, 143)
Talpapellis	1-0-0	(7)
Teratosperma	2-0-0	(143)
Trichoconis	1-0-0	(147)
Trichothecium	0-0-1	(143)
Trimmatostroma		[= *Intralichen*]
Vagnia	1-0-0	(165)
Verrucaster	1-0-0	(148)
Vouauxiella	5-0-0	(2, 148)
Vouauxiomyces		[anam. of *Abrothallus*]
Xanthoriicola	1-0-0	(143, 302)
Zevadia	1-0-0	(59)
Basidiomycota		
Agaricales		
Tricholomataceae		
Fayodia	2-0-0	(9)
Omphalina	1-0-0	(53, 238, 255)
Agaricostilbales		
Chionosphaeraceae		
Chionosphaera	3-0-0	(186, 246, 315)
Boletales		
Coniophoraceae		
Leucogyrophana	1-0-0	(268)
Platygloeales		
Platygloeaceae		
Cystobasidium	2-0-0	(315)
Polyporales		
Atheliaceae		
Athelia	1-0-1	(180, 240, 304, 311)
?Corticiaceae		
Marchandiobasidium	2-0-0	(62, 73, 98, 143, 317) [incl. anam. *Marchandiomyces*]
Tremellales		
Syzygosporaceae		
Syzygospora	3-0-0	(315)
Tremellaceae		
Tremella	46-0-0	(315, 316)
Incertae sedis		
Biatoropsis	1-0-0	(315, 316)

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[1] Numbers of species per genus (lichenicolous fungi-lichenicolous or doubtfully lichenicolous lichens-facultatively or doubtfully lichenicolous fungi).

TABLE 3. Continued.

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[2] (1) Alstrup (1992), (2) Alstrup (1993*a*), (3) Alstrup (1993*b*), (4) Alstrup (1996), (5) Alstrup (1997), (6) Alstrup et al. (1994), (7) Alstrup & Cole (1998), (8) Alstrup & Hansen (2001), (9) Alstrup & Hawksworth (1990), (10) Alstrup & Olech (1993), (11) Alstrup & Olech (1996), (12) Alstrup & Svane (1998), (13) Aptroot (1991), (14) Aptroot et al. (1995), (15) Aptroot el al. (1997), (16) Aptroot & Sipman (2001), (17) Atienza (2002), (18) Atienza & Hawksworth (1994), (19) Awasthi (1991), (20) Barr (1997), (21) Berger (2000), (22) Berger & Diederich (1996), (23) Boqueras & Diederich (1993), (24) Braun (1988), (25) Breuss (1985), (26) Breuss (1990), (27) Breuss (1998), (28) Bricaud & Roux (1991), (29) Cáceres et al. (2001), (30) Calatayud & Atienza (1995), (31) Calatayud & Atienza (2000), (32) Calatayud et al. (1995), (33) Calatayud & Barreno (1995), (34) Calatayud et al. (1997), (35) Calatayud & Etayo (1999*a*), (36) Calatayud & Etayo (l999*b*), (37) Calatayud & Etayo (2001), (38) Calatayud et al. (2001*a*), (39) Calatayud & Navarro-Rosinés (1998), (40) Calatayud & Navarro-Rosinés (2000), (41) Calatayud & Navarro-Rosinés (2001), (42) Calatayud et al. (2000), (43) Calatayud & Rambold (1998), (44) Calatayud & Rico (1995), (45) Calatayud et al. (2001*b*), (46) Calatayud & Triebel (1999), (47) Calatayud & Triebel (2001), (48) Christiansen (1956), (49) Christiansen (1980), (50) Christiansen (1993), (51) Clauzade et al. (1989), (52) Cole & Hawksworth (2001), (53) Collin & Lauron (1994), (54) Constantinescu & Santesson (1987), (55) Coppins (1988), (56) Coppins & Kondratyuk (1995), (57) Coppins & Kondratyuk (1998), (58) David & Etayo (1995), (59) David & Hawksworth (1995), (60) Diederich (1986), (61) Diederich (1989), (62) Diederich (1990), (63) Diederich (1992*a*), (64) Diederich (1992*b*), (65) Diederich (1994), (66) Diederich (1995), (67) Diederich (2002), (68) Diederich & Etayo (1994), (69) Diederich & Etayo (2000), (70) Diederich & Puntillo (1995), (71) Diederich & Scheidegger (1996), (72) Diederich & Scholz (1995), (73) Diederich et al. (2003), (74) Diederich & Sérusiaux (2003), (75) Diederich et al. (2002), (76) Diederich & Zhurbenko (1997), (77) Diederich & Zhurbenko (2001), (78) Earland-Bennett & Hawksworth (1999*a*), (79) Earland-Bennett & Hawksworth (1999*b*), (80) Egea & Torrente (1994), (81) Elenkin & Woronichin (1908), (82) Eriksson et al. (2001), (83) Eriksson & Hawksworth (1986), (84) Eriksson & Hawksworth (1987), (85) Eriksson & Santesson (1986), (86) Etayo (1991), (87) Etayo (1993), (88) Etayo (1994), (89) Etayo (1995a), (90) Etayo (1995*b*), (91) Etayo (1996), (92) Etayo (2000), (93) Etayo (2002), (94) Etayo & Breuss (1998), (95) Etayo & Breuss (2001), (96) Etayo & Calatayud (1998), (97) Etayo & Diederich (1995), (98) Etayo & Diederich (1996*a*), (99) Etayo & Diederich (1996*b*), (100) Etayo & Diederich (1998), (101) Etayo & Diederich (2000), (102) Etayo & Diederich (2001), (103) Etayo et al. (2001), (104) Gierl & Kalb (1993), (105) Giralt & Hawksworth (1991), (106) Grube & Hafellner (1990), (107) Grube & Matzer (1997), (108) Grube et al. (1995), (109) Hafellner (1978), (110) Hafellner (1979), (111) Hafellner (1982*a*), (112) Hafellner (1982*b*), (113) Hafellner (1982*c*), (114) Hafellner (1985*a*), (115) Hafellner (1985*b*), (116) Hafellner (1987*a*), (117) Hafellner (1987*b*), (118) Hafellner (1989), (119) Hafellner (1993), (120) Hafellner (1994*a*), (121) Hafellner (1994*b*), (122) Hafellner (1995), (123) Hafellner (1996*a*), (124) Hafellner (1996*b*), (125) Hafellner (1998*a*), (126) Hafellner (1998*b*), (127) Hafellner (1999), (128) Hafellner (2001), (129) Hafellner & Berger (2000), (130) Hafellner & Calatayud (1999), (131) Hafellner & Obermayer (1995), (132) Hafellner & Poelt (1980), (133) Hafellner & Türk (1995), (134) Hafellner & Wieser (2000), (135) Hansen & Alstrup (1995), (136) Hariharan et al. (1996), (137) Harris (1995), (138) Hawksworth (1975*a*), (139) Hawksworth (1975*b*), (140) Hawksworth (1977*a*), (141) Hawksworth (1977*b*), (142) Hawksworth (1978*a*), (143) Hawksworth (1979*a*), (144) Hawksworth (1979*b*), (145) Hawksworth (1979*c*), (146) Hawksworth (1980*a*), (147) Hawksworth (1980*b*), (148) Hawksworth (1981), (149) Hawksworth (1982*a*), (150) Hawksworth (1982*b*), (151) Hawksworth (1984), (152) Hawksworth (1985), (153) Hawksworth (1986), (154) Hawksworth (1990*a*), (155) Hawksworth (1990*b*), (156) Hawksworth (1991*a*), (157) Hawksworth (1994), (158) Hawksworth & Atienza (1994), (159) Hawksworth & Cole (2002) (160) Hawksworth & Diederich (1988), (161) Hawksworth & Dyko (1979), (162) Hawksworth & Galloway (1984), (163) Hawksworth & Kalb (1992), (164) Hawksworth & Miadlikowska (1997*a*), (165) Hawksworth & Miadlikowska (1997*b*), (166) Hawksworth & Poelt (1986), (167) Hawksworth & Santesson (1988), (168) Hawksworth & Santesson (1990), (169) Henssen (1964), (170) Henssen (1995), (171) Henssen & Kantvilas (1985), (172) Hertel (1969), (173) Hertel & Rambold (1990), (174) Horáková (1994), (175) Horáková & Alstrup (1994), (176) Huhtinen & Santesson (1997), (177) Ihlen (1995), (178) Ihlen (1998), (179) Isbrand & Alstrup (1992), (180) Jülich (1972), (181) Kalb (1990), (182) Kalb (2001), (183) Kalb & Elix (1995), (184) Kalb et al. (1995), (185) Keissler (1930), (186) Kirschner et al. (2001), (187) Kocourková & Berger (1999), (188) Kondratyuk (1996*a*), (189) Kondratyuk (1996*b*), (190) Kondratyuk & Galloway (1995*a*), (191) Kondratyuk & Galloway (1995*b*), (192) Kondratyuk & Galloway (1995*c*), (193) Kondratyuk et al. (1994), (194) Kutorga & Hawksworth (1997), (195) Löfgren & Tibell (1979), (196) Lowen (1995), (197) Lowen et al. (1986), (198) Lücking (1997), (199) Lücking & Sérusiaux (1998), (200) Lumbsch (1989), (201) Martínez & Hafellner (1998), (202) Matzer (1993), (203) Matzer (1996), (204) Matzer & Hafellner (1990), (205) Mayrhofer (1987*a*), (206) Mayrhofer (1987*b*), (207) Ménard & Roux (1991), (208) Miadlikowska & Alstrup (1995), (209) Molitor & Diederich (1997), (210) Moreau (1951), (211) Moreau & Moreau (1951), (212) Muntañola-Cvetkovic & Gómez-Bolea (1998), (213) Navarro-Rosinés et al. (1998*a*), (214) Navarro-Rosinés & Etayo (2001), (215) Navarro-Rosinés et al. (1999), (216) Navarro-Rosinés & Hafellner (1996), (217) Navarro-Rosinés & Hladun (1990), (218) Navarro-Rosinés & Haldun (1994), (219) Navarro-Rosinés & Hladun (1995), (220) Navarro-Rosinés & Roux (1990), (221) Navarro-Rosinés & Roux (1995), (222) Navarro-Rosinés & Roux (1996), (223) Navarro-Rosinés & Roux (1997*a*), (224) Navarro-Rosinés & Roux (1997*b*), (225) Navarro-Rosinés & Roux (1998), (226) Navarro-Rosinés et al. (1998*b*), (227) Navarro-Rosinés et al. (1995), (228) Navarro-Rosinés et al. (1998*c*), (229) Navarro-Rosinés et al. (1996), (230) Navarro-Rosinés et al. (1998*d*), (231) Navarro-Rosinés et al. (1994*a*), (232) Navrotskaya et al. (1996), (233) Nimis et al. (1994), (234) Nordin (1964), (235) Obermayer (1994), (236) Olech & Søchting (1993), (237) Orange (2002), (238) Orton (1977), (239) Øvstedal & Hawksworth (1986), (240) Parmasto (1998), (241) Poelt & Vězda (l981), (242) Purvis et al. (1992), (243) Rambold (1993), (244) Rambold & Triebel (1990), (245) Rambold & Triebel (1992), (246) Roberts (1997), (247) Roux et al. (1994), (248) Roux et al. (1997), (249) Roux & Navarro-Rosinés (1994), (250) Roux & Triebel (1994), (251) Roux et al. (1995), (252) Samuels (1988), (253) Santesson (1988), (254) Santesson (1989), (255) Santesson (1993*a*), (256) Santesson (1993*b*), (257) Santesson (1994*a*), (258) Santesson (1994*b*), (259) Santesson (1998), (260) Santesson & Tønsberg (1994), (261) Scheidegger (1987), (262) Scholz (1998), (263) Sérusiaux et al. (1999), (264) Sérusiaux & Wessels (1984), (265) Sherwood (1977), (266) Sherwood-Pike (1987), (267) Thor (1985), (268) Thorn et al. (1998), (269) Tibell (1971), (270) Tibell (1978), (271) Tibell (1991*a*), (272) Tibell (1991*b*), (273) Tibell (1998), (274) Tibell & Ryman (1995), (275) Timdal (1992), (276) Tretiach & Nimis (1999), (277) Triebel (1989), (278) Triebel & Rambold (1988), (279) Triebel et al. (1995), (280) Triebel et al. (1991), (281) Triebel & Scholz (2001), (282) Triebel et al. (1997), (283) Váczi & Hawksworth (2001), (284) van den Boom et al. (1998), (285) Wedin (1994), (286) Wedin & Hafellner (1998), (287) Wedin & Kondratyuk (1997), (288) Wetmore (1999), (289) Zehetleitner (1978), (290) Zhurbenko et al. (1995), (291) Baral & Marson (2001), (292) Brand (pers. comm.), (293) Cáceres & Lücking (2000), (294) Diederich & Wedin (2000), (295) Diederich et al. (2002), (296) Hafellner (2000), (297) Hafellner & Sancho (1990), (298) Hawksworth (1976), (299) Hawksworth (1978*b*), (300) Hawksworth & Esslinger (1993), (301) Hoffmann & Hafellner (2000), (302) Hawksworth & Punithalingam (1973), (303) Ihlen & Tønsberg (1996), (304) Arvidsson (1976), (305) Kantvilas & Vězda (1992), (306) Lücking (1998), (307) Navarro-Rosinës & Roux (pers. comm.), (308) Olech & Alstrup (1996), (309) Rossman et al. (1999), (310) Roux et al. (1998), (311) Arvidsson (1978), (312) Sutton (1980), (313) Triebel (1993), (314) Punithalingam & Spooner (1997), (315) Diederich (1996), (316) Diederich & Christiansen (1994), (317) Sikaroodi et al. (2001).

TABLE 4. Summary of species numbers from Table 3.

	No. species[1]	Total
Number of Ascomycota	1,031-252-6	1,289
Number of anamorphic Ascomycota	198-1-8	207
Number of Basidiomycota	62-0-1	63
Total	1,291-253-15	1,559

[1] Numbers of species per genus (lichenicolous fungi–lichenicolous or doubtfully lichenicolous lichens–facultatively or doubtfully lichenicolous fungi).

mycetes. Basidiomata of *M. aurantiacus* have recently been discovered, and the new genus *Marchandiobasidium* described for the teleomorph (Diederich et al. 2003).

The discovery of the lichenicolous heterobasidiomycetes in itself was perhaps not a surprise, but the astonishing number of 54 species discovered within just a few years (Diederich 1996) exceeded any expectation. The genus *Tremella* alone numbered 46 species in 1996, and additional, as yet undescribed species are continuously being discovered (Diederich, unpubl.). The genera *Biatoropsis* (with one species) and *Syzygospora* (3 species, including one only provisionally placed there) most probably belong to the Tremellales. All of these genera belong to the Basidiomycetes (Kirk et al. 2001), and all species are strictly host specific.

Two further genera traditionally grouped with the heterobasidiomycetes, *Cystobasidium* and *Chionosphaera*, belong to the Urediniomycetes (Kirk et al. 2001). *Cystobasidium* includes two conspicuous gall-forming species on *Hypogymnia* and *Usnea*. *Chionosphaera*, with several (partly undescribed) lichenicolous species, does not look at all like a basidiomycete, but instead resembles synnemata of a hyphomycete, at the apex of which basidiospores are produced on cylindrical basidia with reduced sterigmata. *Chionosphaera* species are still poorly known, but are likely not to be host specific.

These recent discoveries have greatly expanded the number of basidiomycete species known to associate with lichens. Nevertheless, basidiomycete lichenicolous fungi make up only a small fraction of the group (Table 4). Given the pattern of discovery of new lichenicolous fungi, this is unlikely to change significantly in the future.

Other types.—Keissler (1930) listed a number of facultative lichenicolous fungi belonging to the Myxobacterales (Bacteria) or to the Myxomycota (Protozoa), and one species of Zygomycota (Fungi). All these species are now considered to be non-lichenicolous, although some of them regularly overgrow lichen thalli. An overview of all species of Myxomycetes mentioned in the literature from lichen thalli is given by Clauzade et al. (1989); one species, *Licea parasitica*, is commonly found on corticolous lichens.

BIOGEOGRAPHY AND ECOLOGY

Temperate regions.—Until very recently, lichenicolous fungi had only been intensively studied in Europe. Those from North America were still almost unknown in 1990, but many recent studies, some as yet unpublished, quickly raised the number of species to several hundred, and hundreds of additional North American species still await discovery and description. Temperate regions of Asia, including Japan, are almost entirely unexplored for lichenicolous fungi; one paper by Zhurbenko and Otnyukova (2001) lists 20 species from the Sayan-Tuvan Mountains, southern Siberia, Russia. Lichenicolous fungi from temperate South America were collected in abundance by R. Santesson (material in UPS), and many of these specimens have been published in diverse papers. Just a few species are known from South Africa, including three recently described by Egea and Torrente (1996). In Australia and New Zealand, a relatively small number of species are currently known, but there are recent efforts to collect more of them; the lichenicolous flora in both countries appears to be extremely rich, and hundreds of species are likely to occur there.

Polar regions.—Arctic and subarctic lichenicolous fungi have been intensively sampled and studied during the past 15 years. A major work on the species from Greenland (Alstrup & Hawksworth 1990) listed 124 species. As these authors usually used very broad species concepts, often including material from distinct host genera within the same species, the actual number of taxa represented by their material might even be higher. Additional species from Greenland were published in several subsequent papers e.g., Alstrup et al. (2000) and Alstrup and Hansen (2001). From Spitsbergen, Alstrup and Olech (1993) recorded 29 species, and 50 species are currently known from the Faroes (Alstrup et al. 1994). Several species were mentioned from Iceland by Orange (1990). The Siberian arctic and subarctic has been visited several times by M.

Zhurbenko. His first paper listed 74 species from a region extending from Franz Josef Land to the Chukchi Peninsula (Zhurbenko & Santesson 1996). Later he reported a total of 68 species from north Central Siberia (Zhurbenko 1996, 1998), mainly from the Taimyr peninsula. Most recently Zhurbenko and Hafellner (1999) recorded 47 species from the Putorana plateau in the vicinity of the Taimyr peninsula. The lichenicolous fungi of the northern territories of Canada have hardly been studied. However, those of Alaska were intensively sampled during two recent collecting trips by M. Zhurbenko. One preliminary paper (Zhurbenko et al. 1995) listed 13 species.

All of these studies indicate that the lichenicolous flora in arctic and subarctic regions is very diverse, and it appears reasonable to estimate the number of species occurring there at more than 300. Some genera of lichenicolous fungi are especially well represented in boreal regions. For example, most lichenicolous species of *Odontotrema* studied by Diederich et al. (2002) are from northern countries (Alaska, Iceland, Scotland, Scandinavia, northern Russia). Some host genera well represented in nordic countries are particularly rich in lichenicolous fungi e.g., *Thamnolia* (Ihlen 1995); *Baeomyces, Dibaeis*, and *Icmadophila* (Ihlen 1998); and *Cladonia* (Hansen & Alstrup 1995).

The lichenicolous fungi from antarctic and subantarctic regions are poorly known and no general overview exists. Øvstedal and Hawksworth (1986) recorded five species from Bouvetøya. Other species were published by Diederich (1992), Olech (1994), Olech and Alstrup (1996), and Wedin (1994).

Tropical regions.—Lichenicolous fungi are poorly known in the tropics, although several countries have been sampled intensively after 1990. Following an expedition to Papua New Guinea with A. Aptroot, E. Sérusiaux, and H. Sipman – P. Diederich was able to identify or describe over 80 species (Aptroot et al. 1995, 1997; Diederich 1996, 1997); a considerable number of additional species were collected, but not yet identified. After an expedition to Colombia, Etayo (2002) identified or described 104 species, and the author mentioned the occurrence of more than 40 additional unidentified species. The lichenicolous fungi from Africa, India, and other SE Asian countries are poorly known.

Astonishingly, the lowland rainforests are almost devoid of lichenicolous fungi (with the exception of those growing on foliicolous lichens), and the most common lichens occurring in these forests, such as species of Arthoniaceae, Graphidaceae, Pyrenulaceae, Rocellaceae, Thelotremataceae, and Trichotheliaceae, are rarely infected by any of them. It is only at higher elevations that lichenicolous fungi become more common and diverse. Diederich (1997) reported that the average number of species of lichenicolous fungi present in lowland localities is just one, while at higher elevations, good localities commonly yield 30 or more species. A total of 63 species could be identified from three localities at an elevational range of 2,300–4,200 m in Papua New Guinea (Diederich 1997), while the 104 identified species reported from Colombia (Etayo 2002) are from nine localities at 2,400–3,800 m.

At lower elevations, the foliicolous lichens represent a particular ecological niche for lichenicolous fungi. Matzer (1996) revised those species with fissitunicate asci and accepted approximately 50 species. The recent checklist of all known lichenicolous fungi on foliicolous lichens (Lücking et al. 2000) includes 80 species (Table 5).

Effects of lichenicolous fungi on lichen communities.—Since parasites are known to alter the dynamics of host communities, lichenicolous fungi may have similar effects in lichen communities. However, lichenicolous fungi are rarely sampled in lichen community studies, so there is little information available to answer even the most basic questions. Does lichen community structure change depending on the presence or dominance of lichenicolous fungi? Are measures of species diversity similar for lichens and lichenicolous fungi? Are generalist and specialist lichen parasites different in their effects on lichen communities? Are there differences in the effects of parasites on sexual/asexual lichens? Given the substantial body of theoretical work on host-parasite community ecology, there are a number of general predictions that lichen ecologists may test.

For example, community ecologists have long argued that higher species diversity is expected for communities that harbor parasites (including herbivores) since potentially dominant species should suffer disproportionately high infection (Crawley & Pacala 1991). If this is true for lichens as well, there should be measurable effects of parasites on species dominance in lichen communities. Community ecology theory also suggests that the successful establishment of pathogens in a plant community should depend on its structure. The more unpredictable host distribution is to parasites, the less successful parasite invasions ought to be. Burdon et al. (1989) provided some evidence for the idea that patchiness in plant populations, especially for susceptibility genotypes within the populations, determines the extent and intensity of fungal disease epidemics in plant communities. By the same reasoning, it is argued that certain plant pathogens cannot persist at low host densities. Are simple li-

TABLE 5. Genera of lichenicolous fungi growing on foliicolous lichens (following Lücking et al. 2000), arranged following their phylogenetic position. Numbers indicate the number of species known to grow on foliicolous lichens.

Arthonia Ach.	Arthoniales	9
Enterographa Fée	Arthoniales	1
Mazosia Massal.	Arthoniales	1
Opegrapha Ach.	Arthoniales	14
Paradoxomyces Matzer	Arthoniales	1
Trichophyma Rehm	?Arthoniales	2
Epibryon Döbbeler	Dothideales	1
Hemigrapha (Müll. Arg.) D. Hawksw.	Dothideales	4
Koordersiella Höhn.	Dothideales	3
Keratosphaera H. B. P. Upadhyay	Dothideales	4
Lanatosphaera Matzer	Dothideales	2
Lichenopeltella Höhn.	Dothideales	2
Neocoleroa Petr.	Dothideales	3
Polycoccum Körb.	Dothideales	2
Pyrenidium Nyl.	Dothideales	4
Nectriopsis Maire	Hypocreales	1
Gyalideopsis Vězda	Incertae sedis	3
Roselliniella Vain.	Sordariales	2
Roselliniomyces Matzer & Haf.	Sordariales	1
Teratoschaeta Bat. & O. M. Fonseca	Sordariales	1
Stigmidium Trevis.	Verrucariales	6
Ampullifera Deight.	Hyphomycetes	5
Dictyophrynella Bat. & Cavalc.	Hyphomycetes	1
Hansfordiellopsis Deight	Hyphomycetes	3
Sessiliospora D. Hawksw.	Hyphomycetes	1
Teratosperma Syd.	Hyphomycetes	2
Vouauxiella Petr. & H. Syd.	Coelomycetes	1

chen communities more susceptible than diverse ones to attacks by lichen pathogens?

Investigations of lichen communities varying in species richness indicate that lichenicolous fungi tend to be more specialized and less aggressive in lichen-rich communities. In unpolluted species-rich lichen communities, many lichenicolous fungi are parasymbionts and do not visibly damage the host populations. It is mainly in simplified communities, especially those affected by air pollution, that lichen species are obviously affected. In these cases, necrotrophic species such as *Athelia arachnoidea* and *Marchandiomyces aurantiacus* may dominate the community. In Europe, infections by *Athelia arachnoidea* of the lichen *Lecanora conizaeoides* are especially common, especially in polluted areas. The congeneric (although perhaps unrelated) *Athelia epiphylla* and other common lichenicolous species, *Lichenoconium erodens* and *L. lecanorae*, are also commonly observed on *L. conizaeoides* (Christiansen 1980; Liska 1993).

Athelia arachnoidea is considered especially pathogenic and most likely to dominate lichen communities. It is found on numerous lichens in Europe and North America and can easily be identified by its white arachnoid hyphal strands and brown sclerotia. Arvidsson (1976, 1978) studied the development on lichens in southern Sweden and concluded that it was responsible for the elimination of many lichens, especially during the critical colonizing stages in communities affected by air pollution. Lesions of *A. arachnoides* do not appear to develop rapidly on lichens, however, as Gilbert (1988) found in a two-year study of the pathogen on *Lecanora conizaeoides* in England. He estimated that lesions can expand for 10 years or more, during which time central parts of the lichen thallus exhibit secondary infections of *Lichenoconium erodens* and are sometimes even re-invaded by new *L. conizaeoides* thalli. It appears from these observations that *A. arachnoidea* may dominate lichen communities, especially those simplified by air pollution, but there is little evidence that this pathogen prevents establishment of lichens or significantly alters community structure. Hawksworth (1982*c*) has expressed doubts of this as well, noting that it has not stopped the reinvasion of lichens around London in response to improved air quality (Rose & Hawksworth 1981).

Some species of lichenicolous fungi have smaller distribution ranges than their host lichens, and appear to be more restricted to areas with high biodiversity. For example, Diederich (1991) used the lichenicolous ascomycete *Skyttea nitsckkei* as an indicator of forests with a long historical continuity. This fungus has a much smaller area of distribution than its host *Thelotrema lepadinum* in the study area, and is found only in old-growth forests. Many lichenicolous fungi have such distributions that are useful for identifying forested areas of high conservation value. The reasons for such distributions, however, are not known at present. Are these species simply arriving late to the communities or is there a threshold level of biodiversity that is required for their persistence? Does their presence or absence have significant effects on lichen biodiversity, or is it the opposite?

Finally, it has been suggested that asexual plants are more susceptible to pathogen outbreaks than sexual ones (Burden et al. 1987). The explanation for this is that genetic variation inherent in sexual species would presumably limit the degree to which pathogens can exploit the host species. Is there evidence for a similar pattern in lichen communities? To our knowledge, no studies have ever been designed to test this hypothesis. The common occurrence of lichenicolous fungi on both sexual and asexual lichens would seem to argue against it. However, it would be interesting to see if generalized necrotrophic lichen parasites significantly discriminate between (or cause different levels of damage to) closely related sexual and asexual lichen species.

To answer these basic questions, community studies must be designed to document spatial and demographic patterns of both lichens and lichen parasites. We do not know at present how common parasites are in lichen communities. Are lichen parasites as common as those of plant parasites in plant communities or animal parasites in animal communities? Are the distributions of lichen parasites nonrandom? Do changes in the spatial patterns of lichens cause changes in the distributions of parasites? Do parasites frequently co-occur and if so, what are the underlying reasons for this?

Until sufficient information is collected, these questions must remain unanswered. Still, we regard the following hypotheses worthy of consideration until research can be done:

1) When compared with plant or animal communities, lichen communities will always exhibit lower diversities and absolute numbers of parasites.

2) Lichen communities simplified by pollution or other disturbances will be more prone to attack by generalized necrotrophic parasites.

3) As lichen species diversity increases during normal community development (succession), the diversity of lichen parasites will also increase; the late arriving lichens and parasites will be the rarest since they will tend to have the narrowest ecological amplitudes.

Dispersal ecology.—For any parasitic organism, dispersal from one host to another is vital, so reproductive and dispersal mechanisms determine evolutionary success to a much larger extent in parasites than in free-living organisms. The processes of reproduction and dispersal depend on each other but are not identical. Parasite reproduction involves production of progeny, usually sexual or asexual spores, the dissemination of which permits the maximal exploitation of the present host and increases the potential of encountering a new host. Dispersal involves movement from one host to another and generally makes use of reproductive propagules, especially when a new host is colonized in an entirely different habitat. However, dispersal can also involve invading (growing into) the reproductive/dispersal structures of the host that results in dispersal of the parasite each time the host reproduces.

Since dispersal in lichenicolous fungi is generally a matter of producing propagules and trusting to chance for successful dispersal to new hosts and new communities, various aspects of the dispersal propagules can influence success:

1) Propagule size and number determine distance traveled and likelihood of encountering a new host.

2) Reliance on different propagule vectors (physical–wind, water; biological–animals, plants) increases the likelihood of travel to appropriate host habitats. For example, Fox (1997) hypothesized that conidia of *Xanthoriicola physciae*, a parasite of *Xanthoria parietina*, are transported to lichens by a predatory bug, *Temnosthetus gracilis*, as it searches lichen apothecia for mites.

Most lichenicolous fungi exhibit relatively narrow geographic and host ranges, and many are found only in mature lichen communities, all of which suggests that these organisms are generally limited in their abilities to invade new lichen communities. In such cases, any reproductive/dispersal character that enhances colonization of suitable new hosts will be strongly favored by selection. For this reason, we would generally expect to see the most specialized dispersal systems exhibited by the most host-specific and narrowly distributed of lichenicolous species. For example, many mycopathogens produce spores during the dispersal phase of the host so that when seeds or eggs of the host are dispersed the fungus is able to rapidly colonize. This can be observed in some lichenicolous fungi as well. For example, Pyatt and Harvey (1973) studied the dispersal of the lichenicolous *Muellerella lichenicola*, that occupies an unusual niche in the apothecia of *Caloplaca* species. They found that ascospores of the parasite are produced and dispersed along with ascospores of the mycobiont that would obviously facilitate colonization by the parasite on new thalli of the host.

In those few lichenicolous species that are generalized, broadly distributed, and opportunistic, we would expect to see dispersal systems that are equally generalized. There is not much information at present to test this assumption, but the wide geographic ranges of many of the most generalized of lichenicolous species would argue that dispersal is less problematic in these species. Many widely distributed species (e.g., *Athelia* spp., *Marchandiomyces* spp.) appear to disperse by means of sclerotia, which in these species are certainly viable (they will grow in culture). However, many sclerotial species also produce other reproductive structures (basidiospores, conidia). Also, since fungal sclerotia can function as resistant structures as well as dispersal agents, their adaptive role in lichenicolous fungi is unclear as yet and needs to be tested experimentally. Since the most common and widespread of the known lichenicolous fungi produce sclerotia, it is reasonable to assume that this production is somehow important in the success of these species.

Much remains to be discovered about the reproductive/dispersal tactics of lichenicolous fungi. As information accumulates, the following questions may be asked based on the above discussion:

1) How does dispersability of lichen parasites correlate with parasite host specificity or virulence?

2) How does dispersability of lichenicolous fungi relate to their geographic distributions?

3) What regulates the mode of reproduction (sexual vs asexual, conidial vs sclerotial) in these fungi? How do anamorphs and teleomorphs of the same fungus compare in their use of lichens as hosts? Are there differences in host specificity or virulence?

Lichen parasites and biomonitoring.—Lichens have long been used as environmental biomonitors because so many species are sensitive to pollution. Given this well-established fact, how do lichenicolous fungi respond to changes in air quality? Are these responses useful as environmental indicators?

There are conflicting opinions about this and very little reliable information. Lichenicolous fungi are rarely listed in biomonitoring surveys, although some recent studies have included them. A biomonitoring study done in Spain (Glenn et al. 1995) documented noticeable increases in the number of lichenicolous fungi with increased airborne particulate pollution. Particularly noticeable were damaged lichens that had been colonized by generalized necrotrophs and opportunistic saprotrophs. The investigators demonstrated in laboratory and field experiments that lichen thalli damaged artificially with acid misting developed lesions that were colonized by opportunistic hyphomycete saprotrophs. Typical lichenicolous fungi such as *Lichenoconium erodens*, *Cornutispora lichenicola*, and *Trichonectria rubefaciens* were frequently observed later, suggesting that certain lichenicolous fungi benefit from the lichen damage induced by acidic air pollution. In general, however, lichenicolous fungi seem to be as sensitive to poor air quality as the lichens they colonize. It is interesting that the species exhibiting the greatest reduction with improving air quality are the most host-generalized and virulent species known (*Athelia arachnoidea*, *Vouauxiella lichenicola*), indicating that these species are more pollution-tolerant than other species; they may even be pollution adapted, a result indicated by the study of Glenn et al. (1997).

Clearly, investigations of these responses will contribute enormously to the field of lichen biomonitoring. Obligate and specialized lichenicolous fungi are probably as responsive to pollution as lichens, perhaps even more so. We encourage researchers to take note of lichenicolous fungi in their lichen biomonitoring programs and to design sampling and experimental protocols to test hypotheses such as the following:

1) In general lichen saprotrophs and necrotrophic parasites will benefit the most from polluted conditions; specialized biotrophic parasites will tend to decline.

2) In regions where air quality improvements result in noticeable recovery of the lichen communities, there should also be a measurable increase in the diversity of lichenicolous fungi.

EVOLUTION OF A LICHENICOLOUS HABIT

The wide diversity of obligately lichenicolous fungi indicates that the habit evolved in many different fungal groups. What conditions led to the evolution of lichenicolous fungi? How are lichens, lichenicolous lichens, and lichen parasites related phylogenetically? What contribution does association with lichens make to the evolution of the various modes of nutrition in fungi from different phyla?

Theories concerning origin of a lichenicolous habit.—Several authors have discussed the evolution of a lichenicolous habit in the fungi and speculated on possible evolutionary trends in lichen-associated groups. Hawksworth (1978*c*, 1982*a,b*, 1988*a,b*) has repeatedly emphasized the reticulate nature of these pathways in the fungi, suggesting that the lichenicolous habit is one of several nutritional modes along with lichen forming, parasitism, commensalism, and saprotrophy. This idea is supported by a number of recent phylogenetic analyses of the fungi that appear to show a common switching of nutritional mode in all major fungal clades (Gargas et al. 1995).

Recently Lutzoni et al. (2001) proposed that many major clades of ascomycetes are derived from lichens and that many lichenicolous ascomycetes are therefore also derived from lichen-formers. There is certainly morphological support for this hypothesis (Rambold & Triebel 1992). Lutzoni et al. considered that some of the lichenicolous fungi are transitional between lichenized and other non-lichenized modes of existence. They refer to the lichenicolous habit as a ''half-way house'' that facilitates this transition to any one of a number of different modes of nutrition. Also, since several major clades of ascomycetes presently contain few or no lichens, there must be a mechanism causing the apparent high rates of loss of lichenization. The hypothesis is that lichenicolous fungi are the causes of these high rates of loss. At present, there is very little information to support this hypothesis. Especially needed are phylogenetic studies that include large numbers of lichenicolous taxa. For the hypothesis of Lutzoni et al. to be strongly supported the following basic trends should be seen in many separate lineages:

1) Phylogenetic analyses should commonly show a unidirectional transition from lichen-forming to lichenicolous to other nonlichenized modes of existence (saprotrophic, parasitic, etc.).

2) There should be stronger genetic evidence that lichenicolous ascomycetes commonly have lichen ancestors.

The basidiomycetes include few lichens, but many saprotrophic, parasitic, and mutualistic forms, the latter mainly mycorrhizal. There are also a variety of parasitic lichenicolous forms. For at least one lichenized basidiomycete group, the genus *Omphalina*, the lichen habit appears to have a saprotophic ancestry (Lutzoni & Vilgalys 1995). This appears to be true also for ectomycorrhizal homobasidiomycetes (Hibbett et al. 2000). In contrast, all of the species of the heterobasidiomycete genera *Tremella* and *Syzygospora* are mycoparasites with an unusual tremelloid haustorium (Diederich 1996), indicating that the lichenicolous habit in these fungi evolved from mycoparasitic ancestors. In general, therefore, evolutionary trends among parasitic, saprotrophic, and mutualistic basidiomycetes appear not to be clearly defined, instead showing numerous reversals of nutritional condition.

Speciation and the species concept in lichenicolous fungi.—What is a species? The species concept remains as controversial now as it has ever been, especially when applied to fungi. Mycologists generally accept morphologically different fungal strains as different species, especially if they are spatially or ecologically isolated. For fungi that are parasitic, species are frequently recognized based on different host preferences. For example, fungal pathogens on different host plants are frequently considered separate species that can lead to overestimates of species numbers (Hawksworth 2001). However, it can also mask the presence of cryptic species, biological species hidden within existing morphospecies. According to Hawksworth (2001), these are proving to be commonplace in the fungi and may also prove to be a significant fraction of the undescribed lichenicolous fungi. They may not actually be ''cryptic'' since most are distinguishable morphologically or chemically. A recent example is the study of the lichenicolous genus *Stigmidium* (Roux & Triebel 1994), in which an unexpectedly large number of species could be distinguished using new morphological and chemical characters. In addition, increased use of molecular methods has led to more effective detection of cryptic fungal species even in reasonably well-studied groups. For example, Hawksworth (2001) noted that 75 species were accepted in the genus *Fusarium* in 1990, but according to estimates provided by Kerry O'Donnell the number of species diagnosable using DNA sequence data will eventually approach 300.

Given the high rates of discovery of new fungal species globally, Hawksworth (1991*b*, 2001) estimates that only five percent (ca 75,000) of the estimated 1.5 million fungal species are presently known to science. Are parasitic species an especially abundant fraction of this unknown total? According to Hawksworth and Rossman (1997), parasites of lichens, insects, and plants are a large component of the undescribed fungi, along with cryptic species, named and orphaned species (named but not yet accepted, likely including some ''good'' species), and collected and unidentified species.

It is reasonable to expect many new fungal species to be parasitic. Parasitic groups of organisms are generally more speciose than free-living groups of organisms (Price 1980; Toft 1991). The common explanation for this is Fahrenholz's ''rule''–the more intimate a parasite-host association is, the more dependent the parasite species is on the host and the more likely any speciation event in the host will trigger speciation in the parasite. As Toft (1991) pointed out, extinction rates may sometimes also be lower for parasites than for free-living organisms. This is contrary to textbook claims that parasite evolution inevitably leads to a ''dead end'' when selection leads to narrowly adapted and clonal forms that can no longer respond to environmental changes. In many cases, lower extinction rates may be due to high population stability in especially well-adapted parasites; in others, it may be a lack of competition. In any event, evolution of a parasitic way of life does not automatically lead to higher extinction rates.

Given the apparently high level of host-specificity in lichenicolous fungi, can we assume that conditions generally favor high speciation rates or low extinction rates in these groups? Are groups of lichen parasites very much more speciose than phylogenetically related free-living groups? It has been suggested (Lutzoni & Pagel 1997) that one of the consequences of a transition to mutualism is an accelerated rate of nucleotide substitution. This may lead to accelerated rates of speciation in symbiotic organisms. If symbiosis is a major factor driving speciation, may it also be a factor in the evolution of lichenicolous species?

At present, there are not many obvious examples of genera with lichenicolous and free-living species, but there are some. For example, *Lichenopeltella* has a large number of lichenicolous species (many still undescribed), but also a relatively large number of others. *Odontotrema* has at least 15 lichenicolous species, compared to four species confined to phanerogam leaves or herbaceous stems, and six species inhabiting wood or bark. Unfortunately, not much can be concluded at present from these examples, but they demonstrate that comparisons of lichenicolous and non-lichenicolous relatives, perhaps involving nucleotide substitution rates or genetic similarity, can be done.

A problem with this sort of investigation is the uncertainty about the actual number of species of many lichenicolous groups. Some groups undoubtedly contain as-yet undescribed cryptic species, and the problem is to recognize them. One way to do this is to look at their host-specificities. If we assume that most (perhaps 95% or more) lichenicolous species are confined to monophyletic groups of lichens (single species, single genera, rarely several related genera–*Physcia* and *Physconia*, or *Parmotrema* and *Rimelia*), we could list all known lichenicolous species (currently around 1,500, Table 4) and for each species list the known host genera. For example, in classical taxonomy, *Lichenodiplis lecanorae* is one species. It is known from eight host genera, *Caloplaca*, *Diploschistes*, *Evernia*, *Lecanora*, *Lecidea*, *Lecidella*, *Micarea*, and *Pertusaria*. If we consider that there are at least two distinct species on *Lecanora* and two on *Pertusaria*, this suggests that at least 10 species are hidden in this taxon. Another example is *Endococcus perpusillus*, which according to Triebel (1989) is known from *Lecidella*, *Miriquidica*, *Porpidia*, *Protoblastenia*, *Rhizocarpon*, and *Schaereria*. However, recent taxonomic studies (Brand, pers. comm.; Sérusiaux et al. 1999) have shown that the genus *Endococcus* is extremely speciose, with possibly eight distinct species on *Aspicilia*, four on *Collema*, four on *Miriquidica*, four on *Porpidia*, and seven on *Rhizocarpon*. Finally, the genus *Muellerella* has not yet been revised with modern methods, but we expect it to exhibit a pattern similar to that of *Endococcus*.

All of this obviously requires additional study, but if it is true that many groups of lichenicolous fungi contain undescribed species, the current number of species (1,500) will expand to well over 2,500. If we consider further that outside of Europe, almost nothing is known about lichenicolous fungi, and that a number of recent studies in other continents reveal a majority of undescribed species, then these 2,500 species might well be multiplied by two or three. All of this makes the lichenicolous fungi a potentially rich source of new species, a conclusion reached also by Hawksworth and Rossman (1997).

Based on this discussion, we offer the following hypotheses:

1) Many so-called cryptic species will prove to be distinguishable morphologically so long as all available morphological characters are investigated.

2) Most species of lichenicolous fungi known from several non-related hosts will prove to be heterogeneous, representing several distinct species all of which are host-specific.

3) If a lichenicolous species is specialized on two or several closely related host genera, then these genera will prove to be phylogenetically related and derived recently from a common ancestor.

4) The number of species of lichenicolous fungi will prove to be roughly proportional to the number of lichen genera. By this we mean to suggest that if 10 randomly selected host genera are studied in detail and found to harbor 20 lichenicolous species, then we could expect to find around 200 lichenicolous species on 100 randomly selected hosts, etc. It is based on the assumption that most lichenicolous species have restricted host ranges, and that most are specialized on a host genus, not a host species.

Coevolutionary origin of lichen-parasite interactions.—The literature on parasite-host interactions suggests that coevolution in these organisms is not only possible but common (Price 1980). The basic argument is that the frequency of resistant host individuals will increase in the host population because of strong selection, but that as resistance increases in the host population, parasites capable of overcoming the defense will also be favored by selection and multiply. Coevolution thus presumably leads to an escalating ‘‘arms race’’ between the associated species. However, it is obvious that coevolution can take many forms and involve a variety of evolutionary processes (Futuyma & Slatkin 1983; Thompson 1982, 1989, 1994). Associations may even develop without coevolution playing a role at all.

As Futuyma (1998) has pointed out, coevolution is both a *process* of reciprocal adaptive response, and a *pattern* detected by phylogenetic analysis.

TABLE 6. Examples of host genera or families harboring several congeneric lichenicolous fungi, suggesting that coevolution took place.

Lichenicolous fungi	Hosts	Reference
Abrothallus acetabuli, A. bertianus, A. caerulescens, A. microspermus, A. parmeliarum, A. parmotrematis	*Parmelia s. l.*	Clauzade et al. (1989)
Arthonia badia, A. coriifoliae, A. flavicantis, A. maculiformis, A. minuta, A. pelvetii, A. plectocarpoides, A. pseudocyphellariae, A. santessoniana, A. semi-immersa, A. stictaria, A. subaggregata	*Pseudocyphellaria*	Wedin & Hafellner (1998)
Dactylospora glaucomarioides, D. inquilina, D. parasitica, D. parellaria, D. pertusaricola, D. rimulicola, D. saxatilis	*Ochrolechia, Pertusaria*	Clauzade et al. (1989)
7 species of *Endococcus*, some of which undescribed	*Rhizocarpon*	Brand (pers. comm.), Sérusiaux et al. (1999)
all known *Epicladonia* species, viz. *E. sandstedei, E. simplex* and *E. stenospora*	*Cladonia*	Hawksworth (1981)
all known *Gyrophthorus* species, viz. *G. crustulosae, G. gracilis* and *G. perforans*	*Umbilicaria*	Hoffmann & Hafellner (2000)
Lichenochora constrictella, L. epidesertorum, L. epifulgens, L. epimarmorata, L. epinashii, L. pyrenodesmiae, L. sinapispermae, L. wasseri, L. xanthoriae	*Caloplaca, Fulgensia, Xanthoria*	Navarro-Rosinés & Etayo (2001), Navarro-Rosinés et al. (1998)
Lichenochora galligena, L. obscurioides, L. polycoccoides, L. weillei	*Phaeophyscia, Physcia, Physconia*	Navarro-Rosinés et al. (1998)
Odontotrema intermedia, O. santessonii and *O. thamnoliae*	*Thamnolia vermicularis*	Diederich, Zhurbenko & Etayo (2002)
all known *Phacopsis* species (at least 13)	Parmeliaceae	Triebel, Rambold & Elix (1995)
Plectocarpon arthonioides, P. lambinonii, P. lichenum, P. linitae, P. macaronesiae, P. scrobiculatae	*Lobaria,* incl. *Lobarina*	Aptroot et al. (1997), Diederich & Etayo (1994)
Sphinctrina leucopoda, S. tubiformis and *S. turbinate*	*Pertusaria*	Clauzade et al. (1989)

Theoretically, the process of coevolution results in increased fitness to both parasites and hosts caused by reciprocal genetic changes induced by their interactions. However, this is seldom demonstrated experimentally. Rather, a pattern of phylogenetic tracking of hosts by parasites is manifested as either cospeciation, where speciation takes place simultaneously in hosts and parasites, or parallel cladogenesis, where both host and parasite phylogenies mirror one another over time. However, such patterns can arise by a number of processes unrelated to coevolution (Page 1990, 1993, 1994; Page & Hafner 1996).

Do parasites and hosts actually engage in an escalating ''arms race''? What does this escalation lead to, extinction or stability? What forces besides coevolution might cause extinction or stability? Does coevolution lead to increased host specificity? Does it lead to increased genetic diversification of the associates? If phylogenies of hosts and parasites are correlated, are there documentable constraints on specialization that regulate this? What other mechanisms could be causing phylogenetic tracking? What generates and maintains the genetic diversity necessary for coevolution?

Pirozynski and Hawksworth (1988) discussed the fact that fungi are particularly adept at forming symbiotic associations with other organisms, so that coevolution of fungi with other organisms is likely to be common. Although some of the best examples of gene-for-gene interactions between parasites and hosts have been for plants and fungal pathogens (e.g., Flor 1956), still the reciprocal genetic change expected for coevolutionary systems has only rarely been observed. If lichenicolous fungi have coevolved with their lichen hosts, this should be apparent from results of phylogenetic studies. If it can be shown further that some of the genetic differences among the correlated associates lead to greater host specificity or reduced virulence, then a compelling argument can be made for coevolution.

At present there are no phylogenetic studies available to test this idea. However, there are a number of groups of lichens that harbor congeneric lichenicolous fungi, a possible indication of coevolution (Table 6). These associated groups would appear to offer the best chances of finding evidence of coevolution if it has taken place in lichenicolous fungi.

Detailed phylogenetic analyses of lichen parasites and their associated lichen hosts have not yet been attempted for any group of lichenicolous fungi, although the methods required are not very different from those already used successfully by lichenologists to explore mycobiont-photobiont coevolution (e.g., Piercey-Normore & DePriest 2001). To encourage investigations of this sort, we offer the following hypotheses for testing:

1) Groups of lichens that harbor large numbers of obligate parasites will themselves frequently be diverse, a result expected if coevolution is at work in these groups (Ehrlich & Raven 1964). If coevolution is not operating, phylogenetic tracking will not be evident at all, and there should be no correlation between the number of species in parasite and host groups.

2) In diverse groups of lichen parasites exhibiting wide variations in host specificity, phylogenetic tracking will be strongest in specialists and weakest in generalists.

3) In geographically widespread host-specific species of lichenicolous fungi, genetic variants in parasites will be found to associate with genetically distinct populations of the host lichen; the congruence of the parasite and host phylogenies will indicate the degree to which coevolution is responsible for the genetic patterning.

4) Most species of lichenicolous fungi will prove to be specialized on a particular monophyletic group of lichens, and they will have the same age as the ancestor of this group of lichens.

Evolution of parasite virulence.—The assumption that parasite-host associations coevolve, and that reduced parasite virulence results from this coevolution, is held so strongly in the field of parasitology that it operates as something of a paradigm (Toft & Aeschlimann 1991). The assumption is based on the idea that less virulent genotypes maintain their host longest and ultimately produce more replicates than high virulence genotypes. If this is true, then mild forms of a parasite should evolve from more virulent ancestors.

However, there is abundant evidence for evolution of high parasite virulence, usually in situations where the transmissibility of parasites to new hosts is highest. Since the damage done to the host is normally associated with the production of parasite transmission stages, virulence and transmissibility are usually intertwined. Selection is expected to favor the maximum exploitation of a host when it is relatively easy to get from one host to another (May 1991). May also points out that theoretically, evolution of virulence should take place any time there are many genotypes of a parasite infecting a single host since selection will always favor the genotype that replicates the most, regardless of the effect this has on the host.

Lichenicolous fungi have rarely been studied sufficiently to know much about evolutionary trends in virulence. There have been some discussions of this, however. Hawksworth (1982*c*) hypothesized that a dominant trend in lichenicolous fungi may be toward the evolution of lower virulence over time. However, if the hypothesis of Lutzoni et al. (2001) is true and lichenicolous fungi were initially lichenized, then there would be a trend toward increased virulence in many groups.

Given the tools of molecular biology, investigators should be able to infer the direction of evolution of any character, including parasite virulence, by mapping host associations and virulence types onto a phylogeny of a group of parasites. This has not been attempted yet for lichen parasites, but there are groups of species showing a wide range of virulence types that could be profitably studied. For example, the large lichenicolous genus *Lichenoconium* is made up of species that vary considerably in virulence (Hawksworth 1977).

As information accumulates about lichen virulence, a number of interesting questions can be investigated, for example:

1) What is the cause of virulence in lichen parasites and pathogens?

2) How does virulence differ on the various lichen hosts used by generalist lichen parasites?

3) How does virulence differ among widespread and genetically distinct populations of lichen parasites that specialize on a single lichen host? How does virulence differ among populations of the same parasite that colonize different lichens of the same host genus?

4) In groups of related lichen parasites, does increased virulence represent a remnant character in basal groups or a recently derived character?

Population studies.—Phylogenetic studies can provide evidence about how evolutionary relationships among lichens and lichenicolous fungi developed in the past. However, the precise mechanisms responsible for the origin and evolution of lichen-parasite interactions must ultimately be documented at the population level. Given the tools of modern molecular biology, investigators are now routinely exploring microevolutionary patterns in parasite-host (especially plant-fungal) associations, and the literature is growing steadily. At present, however, lichenicolous fungi have rarely been studied at the population level.

A number of interesting questions can be asked about the population genetics of lichenicolous fungi. Are there obvious differences in the genetic variation of these populations? How different is the genetic variation of host-specialists and host-generalists? Is there evidence of genetic differentiation among populations of lichenicolous fungi that utilize different lichen hosts? Is there evidence of geographic differentiation among populations of widely distributed lichenicolous fungi? Can the presence of lichenicolous fungi indicate anything meaningful about the population genetics of lichen populations they inhabit?

A recent study of *Marchandiomyces corallinus* (Molina, DePriest, & Lawrey, unpubl.) showed that there are distinct genetic differences among geographic populations of this fungus. *Marchandiomyces corallinus* exhibits both a wide geographic distribution (it is collected commonly in North America and Europe) and a broad ecological amplitude (it is found on dozens of different lichens); there are numerous opportunities for genetic differentiation among populations of this fungus. In this case, genetic partitioning appears to be a result of geographic distance rather than host switching. Samples of the fungus were obtained from locations in North America and Europe, and in some locations samples were obtained from different lichen hosts as well. Several methods were used to determine the genotype of sampled fungi. Pairwise tests of mycelial compatibility were used to obtain a general idea of genetic similarity (Fig. 4). Mycelial incompatibility is a genetically determined reaction that fungal mycelia exhibit when they contact genetically different mycelia. Genetically identical (and sufficiently similar) mycelia will anastomose readily when grown together on agar, but genetically incompatible mycelia will form interaction zones (Dyer et al. 2001). Various compatibility groups were discovered for *M. corallinus*, and they appear to be correlated with geographic location. For example, samples from North America formed two compatibility groups, and samples from Europe formed three. However, no compatibility was ever observed between any North American sample and any European sample, indicating that the most distant populations are the most different. Samples from different lichens in the same location were always from the same compatibility group.

In addition to mycelial compatibility, molecular markers (RAPD, ITS rDNA) were used to genotype samples. Molecular data generally support the conclusions of the mycelial compatibility tests. Genetic similarity among geographic populations depends on how distant they are from each other, not which lichen host they colonize. Molecular evidence provides higher resolution of the genetic differences among samples, however. For example, RAPD markers are distinct for each sample, indicating a much higher level of genetic variation in populations than was expected for these asexual fungi.

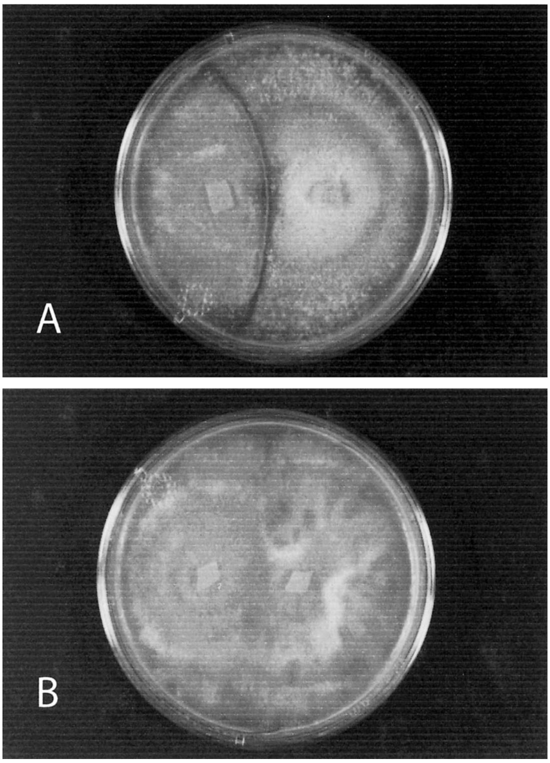

FIGURE 4. Mycelial incompatibility (A) and compatibility (B) exhibited by isolates of *Marchandiomyces corallinus* in culture. — A. Two different isolates (JL160-00 and JL106-95). — B. The same isolate (JL106-95) inoculated twice. Plates are 100 mm diameter.

These results illustrate the sorts of microevolutionary patterns that can be observed in populations of lichenicolous fungi. Such studies can be done using samples obtained from the field and do not require the isolation of the fungal parasites. They can be designed to investigate only the parasites, or to include also the population genetics of the host lichen populations. There are a wide variety of interesting evolutionary hypotheses that can be tested, including the following:

1) Populations of widely distributed, host-generalized species of lichenicolous fungi will be genetically distinct from each other, the differentiation caused mainly by geographic isolation.

2) Genetic differences among populations will reflect various processes of differentiation, including adaptation to new habitats or new hosts, accumulation of random genetic changes in spatially separated populations, mutations in mating and vegetative compatibility genes, etc.

3) Narrowly distributed host specialists will be more genetically uniform than widely distributed generalists.

4) Phylogenetic analyses of speciose groups of specialized parasites will demonstrate that speciation in these parasites is caused more by biotic in-

teractions (coevolution, host-switching) than by spatial separation.

Conclusions

Our approach in this review has been to discuss what is known about lichenicolous fungi, but to also draw attention to what is not known. Our own fascination with these organisms stems from interests in lichens and other fungi, interests we assume are shared by many readers of The Bryologist. The research questions we have posed in this review are questions a lichenologist or mycologist would be expected to ask. What are these fungal associates? How do they live in association with lichens? How do the lichens respond? Certainly there are many fascinating research topics in lichenology and mycology, but we hope readers will now agree that the study of lichenicolous fungi deserves special attention.

As Hawksworth and Rossman (1997) have noted, lichenicolous fungi are probably an important source of new fungal species, and this situation will continue as long as they remain unobserved and uncollected. Lichen collectors who are trained to collect undamaged specimens naturally tend to overlook them. Not too surprisingly, therefore, lichenicolous fungi are relatively under-collected in most regions of the world outside of Europe. North American collections are especially meager. We hope that this review will stimulate the collection of these fungi by North American lichenologists, and that increased attention to these organisms will lead to a better understanding of the roles they play in lichen communities.

Even for frequently collected and well-known species of lichenicolous fungi, however, little is known about their basic biology. We are still almost completely ignorant of their life cycles, ecology, physiology, and biochemistry. The phylogenetic position of many species is still uncertain and the evolutionary trends within lichenicolous groups are still largely unexplored. Questions concerning the systematics and evolution of lichenicolous fungi can now be effectively addressed using the tools of molecular biology, and we expect much will be discovered about these organisms in the near future. As results emerge about these particular fungi, we can expect them to contribute to the broader theoretical discussions about the origin and evolution of parasitism and symbiosis.

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