

Biodiversity of lichens, including a world-wide analysis of checklist data based on Takhtajan's floristic regions

Tassilo Feuerer · David L. Hawksworth

Received: 21 March 2006 / Accepted: 22 November 2006 /
Published online: 17 January 2007
© Springer Science+Business Media B.V. 2006

Abstract The similarity of lichenized fungal species composition among the 35 floristic regions recognized by Takhtajan was calculated, based on checklists of 132 geographical units and a first draft of a global checklist of lichens and allied fungi (which lists 18,882 species) to assess biogeographic and biodiversity patterns of lichenized fungi. A nearest-neighbour cluster analysis of pair-wise comparisons of species composition data (Jaccard index of similarity) from these geographical units is presented. Four main geographical regions were identified: holarctic, subantarctic/Australian, oceanian, and pantropical. Possible changes of the global species number caused by increasing availability of molecular data are discussed. A prospect on future developments of lichen biodiversity research is provided.

Keywords Biodiversity · Distribution areas · Lichens · Lichenized fungi · Molecular data

Introduction

Estimates for the global number of currently recognized lichens range between 13,500 (Hawksworth et al. 1995) and 20,000 when including “orphaned” species (i.e. species which have not, or have only rarely, been recorded after their initial description and are not covered in modern revisions) (Sipman and Aptroot 2001). A precise calculation is confined by several factors: First, species concepts in several groups remain unsettled. Second, there are numerous unresolved taxonomic problems,

T. Feuerer (✉)
Biocentre Klein-Flottbek, Ohnhorststr. 18, 22609 Hamburg, Germany
e-mail: feurerer@botanik.uni-hamburg.de

D. L. Hawksworth
The Yellow House, Calle Aguila 12, Colonia La Maliciosa, Mataelpino, Madrid 28492, Spain
e-mail: myconova@terra.es

especially in crustose lichens. And third, the lichen mycobiota in several areas of the world—especially in the tropics—is still under-explored. Aptroot and Sipman (1997) estimated that 50% of the tropical lichen mycobiota was unknown. A fourth obstacle, the tedious access to data dispersed over a large number of sometimes difficult to obtain publications, is being removed as several major bioinformatic projects come on-line (e.g. Index Fungorum, <http://www.indexfungorum.org>; ITALIC, <http://www.dbiodbs.univ.trieste.it>; LIAS, <http://www.lias.net>). The database which forms the basis of this publication (Feuerer, <http://www.checklists.de>) presently contains 18,882 species, including about 1560 lichenicolous fungi (Lawrey and Diederich 2003).

Among the different scales used to quantify the biodiversity of lichens, gamma diversity, i.e. the species richness of single regions, is the most frequently treated. Structural, chemical and molecular, as well as alpha and beta diversity are less often presented.

Global structure of the biodiversity of lichens

One way to represent the structure of biodiversity on a global scale is through a comparison of the recorded species from distinct floristic regions. An analysis of similarities of lichen diversity and species composition for floristic regions is presented here, following the subdivisions of Takhtajan (1986). This study is similar to the analysis of foliicolous species by Lücking (2003), but is based on a data set of 132 geographical units of all lichens and lichenicolous fungi. The position of the 35 floristic regions is shown in Fig. 1. The similarity of the lichen mycobiotas of the respective units is shown in Fig. 2.

The data used, and the presumptions made, to create the dendrogram include shortcomings of several types. The size and position of the floristic regions proposed by Takhtajan are based on his expert knowledge, instead of calculations, and thus differ from the more recent treatment of global biodiversity of vascular plants by Barthlott et al. (1999). Thus it remains uncertain if the entities described by Takhtajan actually exist as discrete units. In addition, even if these regions can be proven by calculations, it is not known whether lichens belong to the same or similar types of biogeographical units as the floristic regions. The number of checklists used here for the respective compilations is often smaller than desirable. Some compilations include checklists that partly overlap with a neighbouring region and thus obscure the independence of separate regions. The Indian checklist, for instance, covers a considerable part of the neighbouring Sudano-Zambezian Region. Collecting gaps also influence our analysis. These results are therefore preliminary in several respects. As predominantly common and widespread species are generally the first reported from poorly known regions, these floristic regions may appear more similar in the diagram than they actually are. This is counterbalanced to some extent as lists may contain considerable numbers of regional synonyms, so resulting in areas appearing less similar than they are. It is unknown and impossible to estimate in which cases one factor shows a stronger influence on the analysis than the other.

There are areas from which probably more than 95 percent of the existing species are known, e.g. Austria (Hafellner and Türk 2001), Great Britain and Ireland (Coppins 2002), Fennoscandia (Santesson et al. 2004). But from others, e.g. the moist African tropics, only a tiny portion of the actual diversity is recorded. Hawksworth

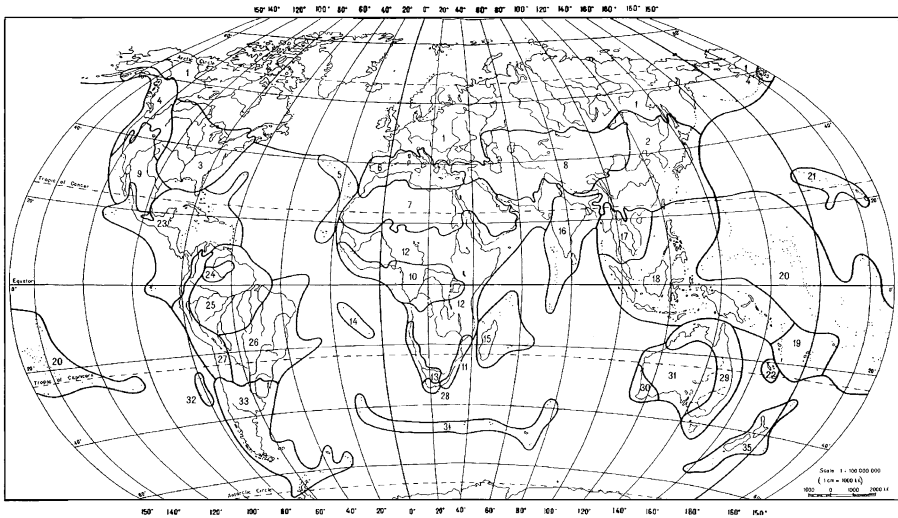


Fig. 1 Floristic regions of the world (Takhtajan 1986). Each floristic region is represented in the analysis by compiled checklists of separate geographical units, with the exception of the Guayana Highlands (24) and the Andean Region (27) which are based on special publications. The original terms of Takhtajan have been used for the single units. 1. Circumboreal Region: Austria, Belgium, Canada: Ontario, Denmark: Mainland, Greenland, Estonia, Finland, Germany, Great Britain, Ireland, Luxembourg, Netherlands, Norway, Poland, Sweden, Switzerland, Svalbard. 2. Eastern Asiatic Region: China: Fujiang, Hebei, Heilongjiang, Hunan, Jiangsu, Jiangxi, Jilin, Shandong, Zhejiang, Japan, Korea, Taiwan. 3. North American Atlantic Region: USA: Alabama, Connecticut, Illinois, Iowa, Louisiana, Michigan, Minnesota, Montana, Mississippi, Missouri, New York, North Carolina, North Dakota, West Virginia, Wisconsin. 4. Rocky Mountain Region: Canada: British Columbia, USA: Washington. 5. Macaronesian Region: Cape Verde Islands, Canary Islands, Madeira, Azores. 6. Mediterranean Region: Algeria, Cyprus, Greece: Crete, Libya, Morocco, Spain, Tunisia. 7. Saharan-Arabian Region: Bahrein, Egypt, Jordania, Kuwait, Mauretania, Qatar, Saudi Arabia. 8. Irano-Turanian Region: Afghanistan, Iran, Tadjikistan. 9. Madrean Region: New Mexico, Utah. 10. Guineo-Congolian Region: Cameroon, Gabon, Ghana, Guinea, Ivory Coast, Liberia, Sierra Leone. 11. Uzambara-Zululand Region: Not treated, data lacking. 12. Sudano-Zambezi Region: Chad, Eritrea, Ethiopia, Kenya, Malawi, Somalia, Tanzania, Zambia, Zimbabwe. 13. Karoo-Namib Region: Namibia. 14. St. Helena and Ascension Region: Ascension, St. Helena. 15. Madagascan Region: Madagascar. 16. Indian Region: India. 17. Indochinese Region: Thailand. 18. Malesian Region: Malaysia, Singapore. 19. Fijian Region: Vanuatu, Solomon Islands, Fiji. 20. Polynesian Region: American Samoa, Cook Islands, Easter Island, Kiribati, Marshall Islands, Tonga. 21. Hawaiian Region: Hawaii. 22. Neocaledonian Region: New Caledonia. 23. Caribbean Region: Bahamas, Costa Rica, Cuba, Dominica, El Salvador, Panama. 24. Region of the Guayana Highlands: Sipman and Aptroot 1992. 25. Amazonian Region and 26. Brazilian Region: Brazil. 27. Andean Region: Sipman 1999. 28. Cape Region: Cape Province. 29. Northeast Australian Region: Queensland, Tasmania, Victoria, New South Wales, Australian Capital Territory. 30. Southwest Australian Region: Western Australia. 31. Central Australian or Eremacan Region: South Australia. 32. Fernándezi Region: Juan Fernandez Island. 33. Chile-Patagonian Region: Chile. 34. Region of the Subantarctic Islands: Bovet Island, South Sandwich Island, South Orkney Island, South Georgia. 35. Neozeylandic Region: New Zealand

and Ahti (1990) provided a bibliographical guide to the treatments of lichens in different countries, and while many more checklists have since been published, there are still 14 countries or other geographical units from which not a single lichen species appears to be known (Feuerer, <http://www.checklists.de>). But even from well-known areas such as central Europe, additional species, even including macrolichens relatively easy to recognize, have recently been described as new

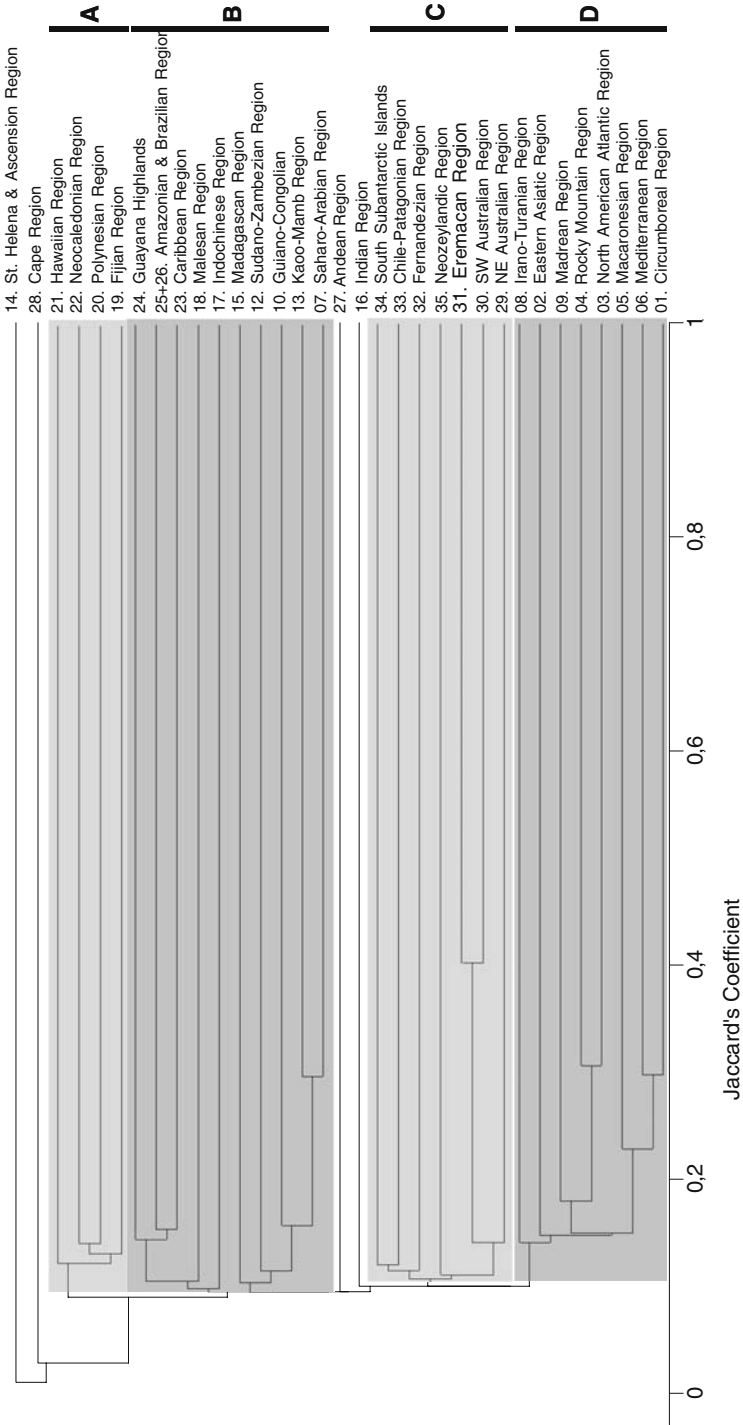


Fig. 2 Similarity dendrogram of lichen gamma diversity for the studied floristic regions recognized by Takhtajan (1986, Fig. 1). A Jaccard cluster analysis based on nearest-neighbour clustering was used to classify data from the 35 regions. The analysis was carried out with the program MVSP Version 3.1 (Kovach 1999). 18,882 species names were included in the analysis

(e.g. *Cladonia monomorpha*, Aptroot et al. 2001; *Parmelia ernstiae*, Feuerer and Thell 2002; *Peltigera monticola*, Vitikainen 1994; *Stereocaulon taeniarum*, Kivistö 1998; three species of *Xanthoria*, Kondratyuk 1997; Kondratyuk and Kärnefelt 1997). In addition, infraspecific taxa have been raised to species level (e.g. *Cetraria obtusata*, van den Boom and Sipman 1994), and formerly synonymized taxa have been resurrected (e.g. *Punctelia ulophylla*, van Herk and Aptroot 2000), thus raising the regional number of species (see also Sipman and Aptroot 2001).

Another issue that needs to be considered when interpreting Fig. 2 is that lichenicolous fungi as well as some non-lichenized microfungi are included in these lists. Lichenicolous and lichen resembling fungi have been included as they are traditionally treated by lichenologists and incorporated into “lichen” checklists. However, we assumed that the results of the similarity calculations of lichens would not be significantly impacted by the small number of these included non-lichens.

The resulting similarity dendrogram indicates the existence of four main biogeographic units (Fig. 2, Clusters A, B, C, D). They correspond to a holarctic unit (D), a subantarctic and an Australian unit (C), a pantropical unit (B), and an Oceanian unit (A). The lichen communities of St Helena and the Cape Region stand apart in this representation because of their restricted sizes. India is not part of the larger clusters as it encompasses very different contrasting elements from the Himalayas and the southern lowland tropical areas. It was interesting to find that the lichens of Pacific islands were not members of the pantropical unit, but formed a separate cluster. On average, each species occurs in 2.2 floristic regions. For foliicolous lichens it has been demonstrated that 40% of the species are distributed on at least two continents (Lücking 2003: 52). These patterns differ from the situation in vascular plants as hypothesized by Takhtajan, in that lichens form fewer but larger discrete biogeographic regions.

“Enigmatic disjunctions” as an essential element of the global biodiversity of lichens

Many lichen species have distribution range sizes and patterns similar to those of vascular plants, but continental disjunctions are much more frequent in lichens. Various authors (e.g. Culberson 1972; Galloway 1992) list some of the types. More and more it is becoming clear that lichen species display almost all possible combinations of continental disjunctions. There are subcosmopolitan (“widespread” sensu Culberson 1972: 166), holarctic (“circumboreal”), pantropical, Europe–North America, eastern North America–Japan and South America–Africa disjunctions, to name the more common ones. Holarctic and pantropical distributions, while more frequent in lichens, are also known from vascular plants. There is a small but interesting group of lichens that displays a bipolar distribution which has been discussed repeatedly (Du Rietz 1926, 1929; Mattick 1950; Galloway and Aptroot 1995). Thell et al. (2002b) demonstrated that almost all bipolar species that have been investigated for their ITS-sequence divergence showed little or no differences between Arctic and Antarctic–subAntarctic samples. Culberson (1972: 167) was aware of the “very large

numbers” of species with “enigmatic disjunctions” citing *Parmotrema latissima* as an example, which he believed to occur only in tropical America and India. Actually, the species grows also in Hawaii, the Marquesas, New Caledonia, the Society Islands and Samoa.

However, there are “enigmatic disjunctions” that appear not to be due to inadequate survey work. These are mostly characterized by having rather large distributional areas in each of the continents where they occur, but an even more enigmatic part of this group of disjunct species shows a normal-sized distributional area in one or more continents but an extremely restricted, point-like distribution in another continent. Some examples of this important type of distribution, which is apparently especially common within the *Parmeliaceae*, are: *Alectoria imshaugii* which grows in a large area on the west coast of North America from south Alberta to northeast California but in Africa it is only known from Gomera and Hierro in the Canary Islands (Østhagen and Krog 1979). *Cetraria odontella* has a large scattered holarctic distribution, is common in Finland and Sweden, but also grows on Mount Kosciuszko in Australia (Thell et al. 2000). *Kaernefeltia merillii* is distributed in North America from southwest Alberta to the Pacific coast and southwards to the Mexican border, but in Europe it is known only from one locality in the central highlands of Spain (Kärnefelt 1980). *Xanthoparmelia pustulosa* is so far only known from a few localities in Colorado and Utah and from Gran Canaria in the Canary Islands (Esslinger 1977). *Xanthoparmelia arida* is widespread in Namaqualand, South Africa, but in addition is known from a few collections in Texas (Hale 1990: 71). *Xanthoparmelia barbatica* ranges from Queensland, New South Wales, and the Australian Capital Territory to Victoria, but is furthermore known only from a single collection from Texas. There are also examples outside the *Parmeliaceae*. *Heterodermia namaquana* has been found in a small area in Namaqualand, South Africa, as well as in southern California and Baja California (Esslinger and Bratt 1998: 31). *Sarcogyne similis* grows in North America and has been recorded from a single locality in Greece by Poelt and Vězda (1974). *Catapyrenium acarosporoides* was considered endemic to the southwestern United States (Thomson 1987), but is now known from a single locality in central Chile (Breuss 1993: 20). *Cladonia halei* is present in the Andes and New Guinea, and *Cladonia signata* in tropical America and Sumatra (Ahti 1993). *Zahlbrucknerella patagonica* has been reported from Patagonia and Antarctica (Henssen 1977) as well as from a single location in Kenya (M. Schultz, pers. com.)

The large fruticose lichen *Coelopogon abraxas* displays an additional and most extreme type of enigmatic disjunct distribution. This member of the *Parmeliaceae* was known only from a mountain top east of Cape Town, South Africa, but has recently been found in a remnant of native forests in central Chile (Thell et al. 2004). In both areas the populations measure only some 100 m in diameter. Also strange is the distribution of *Acroscyphus sphaerophoroides* which is known from 13 small localities in Bhutan, Canada (British Columbia), China (Yunnan), Japan, Mexico, Patagonia, Peru, South Africa, and the USA (Tibell 1996; Joneson and Glew 2003).

All these extremely enigmatic disjunctions were discovered by thorough field-work. It can therefore be expected that many more examples will be detected when the tropics are known as intensively as temperate regions. This additional information would result in an even increased similarity between the lichen mycobiotas of the Takhtajan floristic regions. The traditional hypothesis that fungi show larger distribution areas than phanerogams, or stated differently, that distribution area decreases with increasing complexity of the organism, is thus

confirmed for lichens. It appears likely that lichens even exceed bryophytes (Urmi 1999) in this respect.

The diversity of structural characters in lichens, morphological, anatomical, and cytological should also be considered. Lichens have a smaller number of taxonomically relevant characters than vascular plants. LIAS, for instance, lists over 700 characters (Nash et al. 2002: 638) evidently adequate to describe all known lichens. Ecological significance has been attributed to about 50 of them by various authors (Feuerer, unpubl.). Elix (1993) lists a modest 130 characters as sufficient to characterize all 2300 species of the *Parmeliaceae*. Most characters are, however, “multi-state” and some with a very high number of states; for example more than 1250 alternatives would have to be assigned to the single character “lichen substances” to include all presently known compounds.

Species numbers and “orphaned species”

There are species which have not, or only rarely, been recorded a second time after their initial description, i.e. they are mostly known only from their type locality and many have not been restudied since their original description; further they may be described under generic names no longer in use. Monographs treating them as accepted taxa or synonyms after a thorough revision are often lacking, and some authors omit them from checklists (e.g. Wirth 1994). These “orphaned species” form considerable lists even in several European countries. For example, there are 287 species which are problematic in respect of their ranking as species or their records for the German area, which contains otherwise 2112 species (Scholz 2000). Similar numbers are given for Iceland (Kristinsson 2004, Unpublished Manuscript) and for the Iberian Peninsula and the Balearic Islands (Llimona and Hladun 2001).

Presently there are several projects in different European countries to clarify the status of doubtful species by molecular methods. Many of these doubtful species are common and cited in a high percentage of biodiversity inventories. About 10% of lichens have to be investigated by molecular methods to obtain lists which can be compared without hesitation. However, most orphaned species cannot be easily examined by molecular tools as many of the type specimens are 50–100 or more years old and undamaged DNA is unlikely to be recoverable from them.

Species numbers and molecular data

The preliminary number of 18,882 species of lichens and allied fungi is challenged by the continuously growing availability of molecular data, which leads in some cases to increasing the numbers of species, and in others to reductions in numbers.

One of the mechanisms which leads to an increased number of species is the discovery of cryptic species (e.g. Grube and Kroken 2000). Such species, well-known in non-lichenized fungi (Burt et al. 1996), were discovered first amongst the lichens in *Letharia* during a multilocus study by Kroken and Taylor (2001). This genus of *Parmeliaceae* had traditionally been treated as consisting of a pair of sympatric species, one making abundant sexual structures and the other making few, but it was found to comprise six entities. These authors used as many as 12 variable loci, comprising nuclear ribosomal DNA, chitin synthase I, and 10 anonymous loci, all with

polymorphic nucleotide substitutions. The 10 anonymous loci were developed by performing PCR with nonsense combinations of primers to obtain arbitrary PCR products. The entities, presently not formally described as species, revealed subtle morphological differences. Similarly, differences among ITS sequences were taken as support for the description of new species by Divakar et al. (2005), Feuerer and Thell (2002), Goffinet and Miadlikowska (1999), and Molina et al. (2004). These authors all investigated the variability of sequences of species with large distributional areas. Thus *Parmelia barrenoae* could be separated from the widespread *P. sulcata*, *P. ernstiae* and *P. serrana* from the subcosmopolitan *P. saxatilis*, and the north American *Peltigera phyllidiosa* from the holarctic *P. collina* and *P. neckeri*. It can be expected that many undescribed cryptic species hide in well-known subcosmopolitan macrolichens, but it is interesting that in most cases correlations with previously ignored morphological features occur. In other cases, molecular differences have been found to support the separation of closely related species whose status was previously suspect (Groner and LaGreca 1997; Niu and Wei 1993; Martin and Llimona, 1998).

Articus et al. (2002), however, present evidence that the well-accepted species *Usnea florida* and *U. subfloridana* cannot be separated by molecular data from ribosomal DNA and β -tubulin. Thell and Miao (1999) showed that the formerly well-accepted and morphologically rather distinct *Cetraria ericetorum* can not be separated from *Cetraria islandica* by their ITS sequence.

Another aspect influencing the number of species is the taxonomic rank accorded to chemical races. This topic has been discussed intensely for a long time (e.g. Brodo 1986; Hawksworth 1976; Kärnefelt 1998; Lumbsch 1998a, b; Poelt 1972). Without molecular data, contradicting opinions often stayed implacable. Modern investigations on this subject are too scarce to allow a statistical judgement, but there are examples which either support the splitter or the lumpers factions. For example, *Cetrelia olivetorum* which has been treated as single species (e.g. Santesson et al. 2004) shows sufficient correlation between preliminary ITS sequences and chemical constituents (Thell et al. 2002b: 347) to justify splitting it into four species. *Cladonia mitis* provides an opposite situation, as molecular data from many specimens collected worldwide showed that *Cladonia mitis* forms a clade within *C. arbuscula* (Myllys et al. 2003); the taxonomic ranking of those taxa, which differ mainly by their chemical constituents, has been the subject of an extended dispute (Ruoss 1987 a, b) at last resolved.

The taxonomic evaluation of species pairs (Poelt 1970, 1972) may lead to additional changes in species numbers. Molecular investigations so far suggest that asexual counterparts of species pairs do not form monophyletic groups as predicted, and that there is considerable genetic variation among sexual and asexual members of a species pair (Lohtander et al. 1998; Myllys et al. 1999) showing that they have to be treated as separate species. The only case in which the results of a molecular investigation led to a proposal to fuse two species is not exhaustively treated in our opinion. The species pair concept in *Physcia aipolia* and *P. caesia* was challenged using β -tubulin, ITS and group I intron sequences (Myllys et al. 2001), but the two morphologically and ecologically separated units could not be separated sufficiently with this selection of genes and samples, but are separable using ITS data alone.

Molecular data on phycosymbiodemes may additionally reduce the global number of species. These are fungi which form distinctly different morphological lichens depending on whether their symbiotic partner is a green alga or a cyanobacterium (Renner and Galloway 1982). Using restriction site data of large subunit nuclear

ribosomal DNA, Armaleo and Clerc (1991) suggested ‘near-identity’ of mycobionts associated with different photobionts. Goffinet and Bayer (1997) found that photomorphs of some *Peltigera* species have identical ITS sequences, but they noted that ITS data alone cannot always discriminate between genetically isolated species, a phenomenon again recognized amongst no-lichenized fungi.

To summarize, ITS sequence variation is in many cases sufficient to recognize species. More rarely, intra- or interspecific variation in LSU and SSU has been shown to occur in lichenized fungi (e.g. Myllys et al. 1998; Miadlikowska et al. 2002). All these loci are part of the same co-transcribed gene cluster. In addition, information from β -tubulin, GAPDH, and mitochondrial SSU sequences have been shown to have high utility in species delimitation within *Parmeliaceae* and *Cladoniaceae* (Thell et al. 2004; Crespo et al. 2001; Myllys et al. 2003).

Biogeography and molecular data

A key question in lichen diversity and biogeography studies remains whether disjunct populations from different continents belong to the same species. Molecular methods are now being used to clarify the identity of these populations. In some cases comparison of ITS sequences was sufficient to suggest that specimens from different continents belong to the same species; for example *Cetraria islandica*, *C. sepincola*, *Flavocetraria cucullata*, *F. nivalis* and *Vulpicida pinastri* from Europe and North America (Thell and Miao 1999), *Cetraria aculeata* and *Tuckermanopsis chlorophylla* from Europe, North America, South America and Africa (Thell et al. 2002b), *Platismatia glauca* from Europe, North America and South America, as well as *P. norvegica* from Europe and North America (Thell et al. 1998). Long-distance dispersal is one explanation for these disjunct distribution patterns. Relict populations formed before the break up of Pangea followed by slow evolutionary change is an alternative hypothesis proposed by Kärnefelt (1990), who discussed 8 species of the genera *Caloplaca*, *Cetrariella*, *Coelopogon*, *Umbilicaria*, and *Xanthomendoza*. However, results of molecular analyses from geographically diverse populations of these species have not been published to date, so these two alternative hypotheses for the observed distribution patterns of these species remain untested.

Other biogeographical studies, based on several genetic markers and large to very large sample sizes, have revealed complex genetic population structures or even cryptic species. Printzen and Ekman (2002) used a haplotype network approach to investigate populations of *Cavernularia hultenii*, a species that is disjunctively distributed in Pacific North America, Newfoundland and northwestern Europe. The molecular data from *C. hultenii* suggests that samples from different continents represent unique taxa.

Prospect

What can be expected for the future knowledge on the biodiversity of lichens? Beside the many fascinating and promising possibilities available by new techniques, especially molecular ones, some concerns have to be cited. The first is the problem of obtaining the necessary material from undersampled regions. This is due in part to reduced, or lack of, accessibility to locations due to wars, war-like situations, the

remnants of wars in the form of land mines, and criminal activities. This is true for some countries in Asia, the Near and Middle East, large parts of Africa and many in Central and Latin America. Additionally the availability of more or less fresh samples essential for phylogenetic investigations is becoming very difficult from many regions due to extremely restrictive legislation and controls introduced under the Convention on Biological Diversity. While these laws aim at the conservation and sustainable use of biodiversity of all kinds, in some cases they lead to the same result as wars and crime in making necessary material unavailable for research elsewhere.

Many species are regionally extinct or threatened to different degrees even in areas where sampling is still possible, such as in central and northern Europe (e.g. Wirth *et al.* 1996, Thor 1995). There are probably species which will become extinct before they are even known to science, mostly caused by the rapid destruction of forests but also by changes in atmospheric pollution of various kinds (e.g. ammonium and nitrogen compounds).

An additional concern is the continuity of some internet services currently available free to lichenologists. These include the immensely useful database for lichenological literature “Recent literature of lichens (RLL)” presented on the web by E. Tindal (http://www.toyen.uio.no/botanisk/bot-mus/lav/sok_rll.htm), the collection of checklists of 549 geographical units (Feuerer, <http://www.checklists.de>), as well as Index Fungorum, ITALIC, LIAS (see p. 2), and the index to exsiccates of Triebel & Scholz (<http://www.141.84.65.135/BSM-Mycology/Exsiccatae/ExsiccataeFind.cfm>). All these initiatives rely almost exclusively on one or few people, some without any institutional or other grant support. The larger and more complex these databases are, the more difficult it will be to find one or several persons willing to assume the task of hosting and maintaining these invaluable resources in the long-term.

Concerns on how the tremendous amount of necessary basic descriptive work can be accomplished to achieve a reasonable knowledge of the world’s lichens have been expressed elsewhere by Hawksworth (1994: 120).

Most other aspects of future research on the biodiversity of lichens seem promising and exciting.

Rapid progress can be predicted for several lichenological subdisciplines, including bioinformatics as well as systematics and phylogeny, due to several current bioinformatic initiatives that will summarize our knowledge on the diversity and distribution of lichenized fungi (see above). Online keys, together with detailed descriptions, pictures of the morphology and important anatomical characters, will be available within a few years for most of the species of Europe and North America, as well as parts of other continents.

The existing lists of species, arranged by politically defined areas such as states and provinces, form an important tool for administrative nature protection projects, but have considerable disadvantages compared to natural defined areas. Therefore, one of the next steps should be to produce data-rich point-distribution maps. These maps can then be connected with phylogenetic, morphological, anatomical, climatological, geological, and geographical data sets. When compiled, these products will enable users to mine data to address many questions including the exact location of centres of endemism and the geographical distribution of structural descriptors on a global scale.

A world map of genetic hot spots for lichens, including centres of endemism, is one of the interesting and challenging goals in this decade. Several obstacles have to be overcome. Currently it is unknown what is the optimal size for the basic squares to plot a global map of lichen biodiversity. Squares of 10,000 km and 1 km may

provide quite different results. Larger data sets for maps based on squares of different size are presently available only for parts of Europe (e.g. Seaward 1995, Türk et al. 1998, Wirth 1990).

One of the most essential projects currently being conducted is “Assembling the Fungal Tree of Life” (AFTOL; Lutzoni 2004). It is developing a higher-level phylogenetic framework for all fungi, using molecular and non-molecular characters. Four laboratories are coordinating sequencing and analysis of seven loci from approximately 1500 representative species from all major groups of fungi including lichens, and one laboratory is generating non-molecular characters that have shown promise for higher-level fungal phylogenetics. Web-accessible databases for molecular and non-molecular characters in fungal phylogenetics are also being developed. More than 100 scientists from 23 countries are participating. Provided it can secure sufficient financial support, the AFTOL project will create an invaluable resource for continued and expanded multi-gene datasets at lower taxonomic levels. Thus it will not only supply data to clarify systematic questions but also to resolve taxonomic problems and finally lead to a sound molecular definition of all lichen species and a satisfying global checklist.

Acknowledgements Greg Mueller (Chicago) is thanked for reviewing a previous version of the manuscript, and Robert Lücking (Chicago) for valuable comments on the first draft.

References

- Ahti T (1993) Names in current use in the *Cladoniaceae* (lichen-forming Ascomycetes) in the ranks of genus to variety. In: Greuter W (ed) NCU-2. Names in current use in the families *Trichocomaceae*, *Cladoniaceae*, *Pinaceae*, and *Lemnaceae*. Regnum vegetabile, Koeltz Scientific Books, Königstein, Germany, pp 58–106
- Aptroot A, Sipman HJM (1997) Diversity of lichenized fungi in the tropics. In: Hyde KD (ed) Biodiversity of tropical microfungi. Hong Kong University Press, Hong Kong, pp 93–106
- Aptroot A, Sipman HJM, van Herk CM (2001) *Cladonia monomorpha*, a neglected cup lichen from Europe. *Lichenologist* 33:271–283
- Armaleo D, Clerc P (1991) Lichen chimeras: DNA analysis suggests that one fungus forms two morphotypes. *Exp Mycol* 15:1–10
- Articus K, Mattsson J-E, Tibell L, Grube M, Wedin M (2002) Ribosomal DNA and β -tubulin data do not support the separation of the lichens *Usnea florida* and *U. subfloridana* as distinct species. *Mycol Res* 106:412–418
- Barthlott W, Biedinger N, Braun G, Feig F, Kier G, Mutke J (1999) Terminological and methodological aspects of the mapping and analysis of global biodiversity. *Acta Botanica Fennica* 162:103–110
- Boom PPG van den, Sipman HJM (1994) *Cetraria obtusata* comb. et stat. nov., an overlooked lichen species from the Central Alps. *Lichenologist* 26:105–112
- Breuss O (1993) *Catapyrenium (Verrucariaceae)* species from South America. *Plant Syst Evol* 185:17–33
- Brodo IM (1986) Interpreting chemical variation in lichens for systematic purposes. *Bryologist* 89:132–138
- Burt A, Carter DA, Koenig GL, White TJ, Taylor JW (1996) Molecular markers reveal cryptic sex in the human pathogen *Coccidioides immitis*. *Proc Natl Acad Sci USA* 93:770–773
- Coppins BJ (2002) Checklist of lichens of Great Britain and Ireland. British Lichen Society, London
- Crespo A, Blanco O, Hawksworth DL (2001) The potential of mitochondrial DNA for establishing phylogeny and stabilising generic concepts in parmelioid lichens. *Taxon* 50:807–819
- Culberson WL (1972) Disjunctive distributions in the lichen-forming fungi. *Ann Missouri Bot Gard* 59:165–173
- Divakar PK, Molina MC, Lumbsch HT, Crespo A (2005) *Parmelia barroanae*, a new lichen species related to *Parmelia sulcata* (*Parmeliaceae*) based on molecular and morphological data. *Lichenologist* 37:37–46

- Du Rietz GE (1926) Den subantarctiska florens bipolära element i lichenologisk be lysning. Svensk Bot Tidskr 20:299–303
- Du Rietz GE (1929) The discovery of an arctic element in the lichen-flora of New-Zealand and its plant geographical consequences. Aus Asso Adv Sci, Report of the Hobart Meeting 1928:628–635
- Elix JA (1993) Progress in the generic delimitation of *Parmelia* sensu lato lichens (*Ascomycotina: Parmeliaceae*). Bryologist 96:359–383
- Esslinger TL (1977) A chemosystematic revision of the brown *Parmeliae*. J Hattori Bot Lab 42:1–211
- Esslinger TL, Bratt C (1998) The *Heterodermia erinacea* group in North America, and a remarkable new disjunct distribution. In: Glenn MG, Harris RC, Dirig R, Cole MS (eds) Lichenographia Thomsoniana: North American Lichenology in Honour of John W. Thomson, Mycotaxon, Ithaca, New York, pp 25–36
- Feuerer T, Thell A (2002) *Parmelia ernstiae* – a new macrolichen from Germany. Mitt Inst Allg Bot Hamburg 30–32:49–60
- Galloway DJ (1992) Biodiversity: a lichenological perspective. Biodivers Conserv 1:312–323
- Galloway DJ, Aptroot A (1995) Bipolar lichens: a review. Cryptog Bot 5:184–191
- Goffinet B, Bayer R (1997) Characterization of mycobionts of phototype pairs in the *Peltigerineae* (lichenized ascomycetes) based on ITS sequences of specifically amplified fungal ribosomal DNA. Fung Genet Biol 21:228–237
- Goffinet B, Miadlikowska J (1999) *Peltigera phyllidiosa* (*Peltigeraceae, Ascomycotina*), a new species from the Southern Appalachians corroborated by ITS sequences. Lichenologist 31:247–265
- Groner U, LaGreca S (1997) The ‘mediterranean’ *Ramalina pannizzei* north of the Alps: morphological, chemical and nrDNA sequence data. Lichenologist 29:441–454
- Grube M, Kroken S (2000) Molecular approaches and the concept of species and species complexes in lichenized fungi. Mycol Res 104:1284–1294
- Hafellner J, Türk R (2001) Die lichenisierten Pilze Österreichs – eine Checkliste der bisher nachgewiesenen Arten mit Verbreitungsangaben. Stapfia 76:3–167
- Hale ME (1990) A synopsis of the lichen genus *Xanthoparmelia* (Vainio) Hale (*Ascomycotina: Parmeliaceae*). Smithsonian Contr Bot 74:1–250
- Hawksworth DL (1976) Lichen chemotaxonomy. In: Brown DH, Hawksworth DL, Bailey RH (eds) Lichenology: progress and problems. Academic Press, London, pp 139–184
- Hawksworth DL (1994) The recent evolution of lichenology: a science for our times. Cryptog Bot 4:117–129
- Hawksworth DL, Ahti T (1990) A bibliographic guide to the lichen floras of the world. (2nd edn). Lichenologist 22:1–78
- Hawksworth DL, Kirk PM, Sutton BC, Pegler DN (1995) Ainsworth and Bisby’s dictionary of the fungi. 8th edn. CAB International, Wallingford
- Henssen A (1977) The genus *Zahlbrucknerella*. Lichenologist 9:17–46
- Joneson S, Glew KA (2003) *Acroschyphus* (*Caliciaceae*) in North America. Bryologist 106:443–446
- Kärnefelt I (1980) Lichens of western North America with disjunctions in Macaronesia and West Mediterranean region. Bot Not 133:569–577
- Kärnefelt I (1990) Evidence of a slow evolutionary change in the speciation of lichens. Bibl Lichenol 38:291–306
- Kärnefelt I (1998) *Teloschistales* and *Parmeliaceae* – a review of the present problems and challenges in lichen systematics at different taxonomic levels. Cryptog Bryol Lichénol 19:93–104
- Kivistö L (1998) Taxonomy of *Stereocaulon paschale* and allied species in Finland. Sauteria 9:25–36
- Kondratyuk S, Kärnefelt I (1997) Notes on *Xanthoria* Th. Fr. II. *Xanthoria poeltii*, a new lichen species from Europe. Lichenologist 29:425–430
- Kondratyuk S (1997) Notes on *Xanthoria* Th. Fr. III. Two new species of the *Xanthoria candelaria* group. Lichenologist 29:431–440
- Kovach WL (1999) MVSP – A multivariate statistical package for Windows, ver. 3.1. Kovach Computing Services, Pentraeth, Wales, United Kingdom
- Kroken S, Taylor JW (2001) A gene genealogical approach to recognize phylogenetic species boundaries in the lichenized fungus *Letharia*. Mycologia 93:38–53
- Lawrey JD, Diederich P (2003) Lichenicolous fungi: interactions, evolution, and biodiversity. Bryologist 106:80–120
- Llimona X, Hladun NL (2001) Checklist of the lichens and lichenicolous fungi of the Iberian Peninsula and Balearic Islands. Bocconeia 14:1–581
- Lohtander K, Källersjö M, Tehler A (1998) Dispersal strategies in *Roccellina capensis* (*Arthoniales*). Lichenologist 30:341–350

- Lücking R (2003) Takhtajan's floristic regions and foliicolous lichen biogeography: a compatibility analysis. *Lichenologist* 35:33–54
- Lumbsch HT (1998a) Taxonomic use of metabolic data in lichen-forming fungi. In: Frisvad JC, Bridge PD, Arora DK (eds) *Chemical fungal taxonomy*. Marcel Dekker, New York pp 345–387
- Lumbsch HT (1998b) The use of metabolic data in lichenology at the species and subspecies levels. *Lichenologist* 30:357–367
- Lutzoni F, Kauff F, Cox CJ, McLaughlin D, Celio G, Dentinger B, Padamsee M, Hibbett D, James TY, Baloch E, Grube M, Reeb V, Hofstetter V, Schoch C, Arnold AE, Miadlikowska J, Spatafora J, Johnson D, Hambleton S, Crockett M, Shoemaker R, Sung G-H, Lücking R, Lumbsch T, O'Donnell K, Binder M, Diederich P, Ertz D, Gueidan C, Hall B, Hansen K, Harris RC, Hosaka K, Lim Y-W, Liu Y, Matheny B, Nishida H, Pfister D, Rogers J, Rossman A, Schmitt I, Sipman H, Stone J, Sugiyama J, Yahr R, Vilgalys R (2004) Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. *Amer J Bot* 91:1446–1480
- Martin MP, Llimona X (1998) Molecular evidence supports the separation of *Teloschistes lacunosus* from *T. villosus*. In: Grube M, Wedin M (eds) *Progress in molecular studies of lichens*: Graz, 11–15 August 1998. Programme and Abstracts, p 19
- Mattick F (1950) Das Problem der bipolaren Flechten. *Polarforsch* 1950:341–345
- Miadlikowska J, McCune B, Lutzoni F (2002) *Pseudocyphellaria perpetua*, a new lichen from Western North America. *Bryologist* 105:1–10
- Molina M del C, Crespo A, Blanco O, Lumbsch HT, Hawksworth DL (2004) Phylogenetic relationships and species concepts in *Parmelia* s. str. (*Parmeliaceae*) inferred from nuclear ITS rDNA and -tubulin sequences. *Lichenologist* 36:37–54
- Myllys L, Lohtander K, Källersjö M, Tehler A (1999) Applicability of ITS data in *Roccellaceae* (*Arthoniales*, *Euascomycetes*) phylogeny. *Lichenologist* 31:461–476
- Myllys L, Stenroos S, Thell A, Ahti T (2003) Phylogeny of bipolar *Cladonia arbuscula* and *Cladonia mitis* (*Lecanorales*, *Euascomycetes*). *Molec Phylogenet Evol* 27:58–69
- Myllys L, Källersjö M, Tehler A (1998) A comparison of SSU nrDNA and morphological data in *Arthoniales* (*Euascomycetes*) phylogeny. *Bryologist* 101:70–85
- Myllys L, Lohtander K, Tehler A (2001) β -tubulin, ITS and group I intron sequences challenge the species pair concept in *Physcia aipolia* and *P. caesia*. *Mycologia* 93:335–343
- Nash TH, Gries C, Rambold G (2002) Lichen floras: past and future for North America. *Bryologist* 105:635–640
- Niu Y, Wei J (1993) Variations in ITS sequences of nuclear nrDNA from two *Lasallia* species and their systematic significance. *Mycosystema* 6:25–29
- Østhaugen H, Krog H (1979) *Alectoria imshaugii* in the Canary Islands. *Norweg J Bot* 26:283–284
- Poelt J (1970) Das Konzept der Artenpaare bei den Flechten. *Vortr Gesamtgeb Bot N F* 4:187–198
- Poelt J (1972) Die taxonomische Behandlung von Artenpaaren bei den Flechten. *Bot Not* 125:77–81
- Poelt J, Vězda A (1974) *Sarcogyne similis*, eine "nordamerikanische" Flechte in Griechenland. *Ann Mus Goulandris* 2:49–54
- Printzen C, Ekman S (2002) Genetic variability and its geographical distribution in the widely disjunct *Cavernularia hultenii*. *Lichenologist* 34:101–111
- Renner B, Galloway DJ (1982) Phycosymbiodemes in *Pseudocyphellaria* in New Zealand. *Mycotaxon* 16:197–231
- Ruoss E (1987a) Chemotaxonomische und morphologische Untersuchungen an den Rentierflechten *Cladonia arbuscula* und *C. mitis*. *Bot Helv* 97:239–263
- Ruoss E (1987b) Species differentiation in a group of reindeer lichens (*Cladonia* subg. *Cladina*). *Bibl Lichenol* 25:197–206
- Santesson R, Moberg R, Nordin A, Tønnsberg T, Vitikainen O (2004) Lichen-forming and lichenicolous fungi of Fennoscandia. Museum of Evolution, Uppsala University
- Scholz P (2000) Katalog der Flechten und flechtenbewohnenden Pilze Deutschlands. *Schriftenreihe Vegetationsk* 31:1–298
- Seaward MRD (ed) (1995) *Lichen Atlas of the British Isles*. Fascicle 1. British Lichen Society, London
- Sipman HJM (1999) Lichens. In: Luteyn JL (ed) *Páramos: a checklist of plant diversity, geographical distribution, and botanical literature*. *Mem New York Bot Gard* 84:41–53
- Sipman HJM, Aptroot A (1992) Results of a botanical expedition to Mount Roraima, Guyana. II. Lichens. *Trop Bryol* 5:79–107
- Sipman HJM, Aptroot A (2001) Where are the missing lichens? *Mycol Res* 105:1433–1439
- Takhtajan A (1986) *Floristic regions of the world*. University of California Press, California
- Thell A, Berbee M, Miao V (1998) Phylogeny within the genus *Platismatia* based on rDNA ITS sequences (lichenized Ascomycota). *Cryptog Bryologie-Lichénologie* 19:307–319

- Thell A, Miao V (1999) Phylogenetic analysis of ITS and group I intron sequences from European and American samples of cetrarioid lichens. *Ann Bot Fenn* 35:275–286
- Thell A, Stenroos S, Myllys L (2000) A DNA-study of the *Cetraria aculeata* and *C. islandica* groups. *Folia Crypt Estonica* 36:95–106
- Thell A, Stenroos S, Feuerer T, Kärnefelt I, Myllys L, Hyvönen J (2002b) Phylogeny of cetrarioid lichens (*Parmeliaceae*) inferred from ITS and β -tubulin sequences, morphology, anatomy and secondary chemistry. *Mycol Progr* 1:335–354
- Thell A, Feuerer T, Kärnefelt I, Myllys L, Stenroos S (2004) Monophyletic groups of the *Parmeliaceae* identified by ITS rDNA, β -tubulin and GAPDH sequences. *Mycol Progr* 3:297–314
- Thomson JW (1987) The lichen genera *Catapyrenium* and *Placidlopsis* in North America. *Bryologist* 90:27–39
- Thor G (1995) Red lists – aspects of their compilation and use in lichen conservation. In: Scheidegger C, Wolseley PA, Thor G (eds) Conservation biology of lichenised fungi Mitt. Eidgen. Forschungsanstalt, Birmensdorf, Switzerland, pp 29–39
- Tibell L (1996) *Caliciales*. *Flora Neotropica* 69. New York Botanical Garden, New York
- Türk R, Breuss O, Üblagger J (1998) Die Flechten im Bundesland Niederösterreich. *Wiss Mitt Niederösterr Landesmuseum* 11:1–315
- Urmí E (1999) Über die relative Grösse von Arealen bei Kryptogamen und Phanerogamen. *Hausknechtia Beih.* 9 (Riclef-Grolle-Festschrift): 377–389
- van Herk CM, Aptroot A (2000) The sorediate *Punctelia* species with lecanoric acid in Europe. *Lichenologist* 32:233–246
- Vitikainen O (1994) Taxonomic revision of *Peltigera* (lichenized *Ascomycotina*) in Europe. *Acta Bot Fenn* 152:1–96
- Wirth V (1990) Initiation of a European lichen mapping project – Proposals and considerations. *Stuttgarter Beitr Naturk Ser A* 456:185–148
- Wirth V (1994) Checkliste der Flechten und flechtenbewohnenden Pilze Deutschlands – eine Arbeitshilfe. *Stuttgarter Beitr Naturk Serie A* 517:1–63
- Wirth V, Schöller H, Scholz P, Ernst G, Feuerer T, Gnüchtel A, Hauck M, Jacobsen P, John V, Litterski B (1996) Rote Liste der Flechten (Lichenes) der Bundesrepublik Deutschland. *Schriftenreihe Vegetationsk* 28:307–368