Abstract Parmelioid lichens are a diverse and ubiquitous group of foliose lichens. Generic delimitation in parmelioid lichens has been in a state of flux since the late 1960s with the segregation of the large, heterogeneous genus Parmelia into numerous smaller genera. Recent molecular phylogenetic studies have demonstrated that some of these new genera were monophyletic, some were not, and others, previously believed to be unrelated, fell within single monophyletic groups, indicating the need for a revision of the generic delimitations. This study aims to give an overview of current knowledge of the major clades of all parmelioid lichens. For this, we assembled a dataset of 762 specimens, including 31 of 33 currently accepted parmelioid genera (and 63 of 84 accepted genera of Parmeliaceae). We performed maximum likelihood and Bayesian analyses of combined datasets including two, three and four loci. Based on these phylogenies and the correlation of morphological and chemical
characters that characterize monophyletic groups, we accept 27 genera within nine main clades. We re-circumscribe several genera and reduce Parmelia to synonymy with Parmotrema. Emodomeleiella Divakar & A. Crespo is described as a new genus (type: E. masonii). Nipponoparmelia (Kurok.) K.H. Moon, Y. Ohmura & Kashiw. ex A. Crespo & al. is elevated to generic rank and 15 new combinations are proposed (in the genera Flavoparmelia, Parmotrema, Myelochroa, Melanelia and Nipponoparmelia). A short discussion of the accepted genera is provided and remaining challenges and areas requiring additional taxon sampling are identified.

**Keywords** combined analysis; Emodomeleiella; generic concept; Lecanorales; large-scale phylogeny; lichens; lichenized fungi; Nipponoparmelia; Parmeliaceae; Parmotrema; taxonomy

**Supplementary Material** Figures S1–S2 and the Appendix are available in the free Electronic Supplement to the online version of this article (http://www.ingentaconnect.com/content/iapt/tax).

## INTRODUCTION

The delimitation of genera in lichen-forming fungi has been in a state of flux since the late 1960s (Poelt, 1966; Hale, 1984b; Elix, 1993; Nimis, 1998; DePriest, 1999) with Parmeliaceae being a prominent example of this. No other group of lichenized ascomycetes was the subject of such vigorous and controversial debates about the recognition and circumscription of genera than these common foliose lichens. Parmeliaceae have mostly foliose, dorsiventral thalli, usually with rhizines on the lower surface, laminal pycnidia and apothecia, Lecanora-type asci and simple hyaline ascospores (Crespo & al., 2001, 2007). With the exception of one study (Thell & al., 2004) that had Parmeliaceae fall into two separate groups, phylogenetic studies converged on one monophyletic core group of Parmeliaceae (Crespo & al., 2001, 2007; Blanco & al., 2006). Parmeliaceae represent the largest group within Parmeliaceae, including about 75% of the described species in this family, which is among the largest families of lichen-forming fungi with nearly 2500 species (Kirk & al., 2008). The Parmeliaceae group comprises common and well-known species, such as Parmelia sulcata, Flavoparmelia caperata, Parmotrema perlatum, and Punctelia subrudecta, which are frequently used in biomonitoring studies of atmospheric pollution (Crespo & al., 1999b, 2004; Nimis & al., 2002). Besides the typical foliose growth forms, some genera with deviating morphologies, such as the peltate Omphalodella, subcrustose Karoowia, subfruticose Almbornia and umbilicate Xanthomaculina have been shown to belong to the Parmeliaceae lichens (Esslinger, 1981; Hale, 1985, 1989; Henssen, 1991; Thell & al., 2006). Recent molecular studies added Parmeliopsis, Cetraria and Parmelaria (previously recognized as cetrarioid lichens), and even the lichenicolous fungus Nesolechia, to the Parmeliaceae clade (Persöö & Rambold, 2002; Blanco & al., 2004a, 2005; Crespo & al., 2007). As taxa were added to the Parmeliaceae clade, taxa that were seen as typical Parmeliaceae lichens, such as Allantoparmelia, Arctoparmelia, Melanelia s.s., and Psiloparmelia, have been found to belong to non-parmelioid groups (Crespo & al., 2007).

Traditional generic classification within Parmeliaceae has relied mostly on morphological and chemical characters of the thallus (Hale, 1974, 1984a, 1986a,b, 1988; Elix & Hale, 1987; Elix, 1993; Crespo & al., 1999a; Divakar & Upreti, 2005a). Acceptance of new genera, segregated from established genera of Parmeliaceae in the absence of ascomatal characters has not been uniform (Poelt & Vězda, 1981; Clauzade & Roux, 1986; Eriksson & Hawksworth, 1986; Purvis & al., 1992; Llimona & Hladun, 2001). Based on the late Mason Hale’s 30-year study of Parmeliaceae, DePriest (1999) gave an overview of his generic delimitation of Parmeliaceae. Hale recognized 36 genera in this group. Subsequently, some of these genera were included within other genera based on morphological and/or molecular evidence. These include Rimeliella, which was placed into synonymy with Canomaculina (Elix, 1997); Almbornia, Chondropsis, Namakwa, Paraparmelia, Neofuscelia, and Xanthomaculina, which were included in Xanthoparmelia (Hawksworth & Crespo, 2002; Elix, 2003; Blanco & al., 2004b; Thell & al., 2006); and Canomaculina, Concamerella, and Rimelia, which were merged with Parmotrema (Blanco & al., 2005). Recently, two additional generic names (Omphalodiella, Placoparmelia) were added as synonyms of Xanthoparmelia (Amo & al., 2010a) and Karoowia was shown to be highly polyphyletic and nested within Xanthoparmelia as well (Amo & al., 2010b). Other genera were found to be polyphyletic, such as Melanelia (Blanco & al., 2004a), which fell into four distinct clades, two of which were recognized as new genera (Melanelia and Melanokoala). Hypotrachyna provides another example, with Cetrariastrum, Everniastrum and Parmelinopsis clustered within a core group of Hypotrachyna, whereas a second group of Hypotrachyna formed a sister clade with Bulbothrix and Parmelinella (Divakar & al., 2006). The latter Hypotrachyna clade was subsequently segregated as Remototrachyna (Divakar & al., 2010). Similarly, an Australasian clade of Parmelia was described as a new genus—Austroparmelia (Crespo & al., 2010).

Although several studies have addressed generic delimitations of Parmeliaceae lichens, the scope of these studies was limited to smaller groups of genera. With the exception of a checklist of European species (Hawksworth & al., 2008), a modern synthesis of the generic classification of Parmeliaceae lichens, summarizing results from molecular phylogenetic studies is still lacking. To fill this gap, we initiated a collaborative research project (PARSYS, Parmelioid systematics) to assemble the largest and most inclusive dataset of DNA sequences of Parmeliaceae lichens to date to address the generic classification within this group.

Specifically, this study aimed at: (1) elucidating evolutionary-ary relationships among Parmeliaceae lichens with phylogenetic
analyses of a four-locus (the nuclear \textit{RPB1} protein-coding gene, and the nuclear ITS, nuclear LSU, and mitochondrial SSU rDNA) dataset including 762 samples representing 470 species including almost all currently accepted genera; (2) providing a comprehensive and coherent classification at the generic level for parmelioid lichens reflecting current knowledge of phylogenetic relationships and giving a short morphological and chemical characterization of monophyletic genera; and (3) identifying generic groups that need additional molecular and morphological work before taxonomic changes can be proposed.

\section*{Materials and Methods}

**Molecular methods.** — Samples prepared from freshly collected, frozen samples or herbarium specimens were ground with sterile glass pestles. Total genomic DNA was extracted using the DNeasy Plant Mini Kit (Qiagen) according to the manufacturer’s instructions and 1–25 ng genomic DNA was used for PCR amplifications of the internal transcribed spacer (ITS) and the genes coding for the nuclear LSU rRNA, mitochondrial SSU and the protein-coding \textit{RPB1} gene, respectively. Primers for amplification were: (i) for the nuclear LSU rDNA: nu-LSU-0155–5’ (Döring \\& al., 2000), nu-LSU-0042–5’ (= LR0R) (Vilgalys, unpub., http://www.botany.duke.edu/fungi/mycolab), AL2R (Mangold \\& al., 2008), nu-LSU-1432–3’ (= LR7), LR5 and nu-LSU-1125–3’ (= LR6) (Vilgalys \\& Hester, 1990); (ii) for the nuclear ITS rDNA: ITS1F (Gardes \\& Bruns, 1993), ITS4 (White \\& al., 1990) and ITS1-LM (Myllys \\& al., 1999) and ITS2-KL (Lohtander \\& al., 1998); (iii) for the mitochondrial SSU rDNA: mrSSU1 and mrSSU3R (Zoller \\& al., 1999), and MSU7 (Zhou \\& Stanosz, 2001), and (iv) for \textit{RPB1} nuDNA: gRPB1-A (Stiller \\& Hall, 1997) and fRPB1-C (Matheny \\& al., 2002), and RPr2 (Wirtz \\& al., 2008). The 25 µL PCR reactions contained 1× buffer (containing 10 mM Tris pH 9.0, 2.5 mM MgCl\textsubscript{2}, 50 mM KC\textsubscript{l}, 0.1% TritonX-100), 0.2 mM each dNTP, 0.5 µM each primer, 1.25 units Taq DNA polymerase (Applied Biosystems) and 1–10 ng genomic DNA extract. Alternatively, amplifications were performed in 50 µL volumes containing a reaction mixture of 5–25 ng genomic DNA, 1× DNA polymerase buffer (Bioloools) (containing 2 mM MgCl\textsubscript{2}, 10 mM Tris-HCl pH 8.0, 50 mM KCl, 1 mM EDTA, 0.1% Triton X-100), 0.2 mM each dNTP, 0.5 µM each primer and 1.25 units DNA polymerase (Biotorools). PCR products were sequenced using the ABI Prism\textsuperscript{TM} Dye Terminator Cycle Sequencing Ready reaction kit (Applied Biosystems) was used with the following settings: denaturation for 3 min at 94°C and 25 cycles at: 96°C for 10 s, 50°C for 5 s and 60°C for 4 min. Sequencing reactions were electrophoresed on a 3730 DNA analyser (Applied Biosystems). Sequence fragments obtained were assembled with SeqMan v.4.03 (DNASTar) and manually adjusted.

**Taxon sampling.** — Data collection across all participants of the PARSYS project was facilitated using a web site (Zope 2.10.4) and an SQL database (Postgresql 8.2.4). Sequences which were newly generated for PARSYS were complemented with sequence data from GenBank (www.ncbi.nlm.nih.gov), using several scripts in the Python programming language (www.python.org) with modules provided from Biopython (Cock & al., 2009) to download and filter the available data. First, all available sequences belonging to Parmeliaceae and the genus \textit{Phacopsis} (according to NCBI’s taxonomy browser), plus sequences from the genus \textit{Protoparmelia} as outgroup, were downloaded from GenBank. The choice of outgroup follows Crespo & al. (2007). Second, the downloaded data were filtered for sequences belonging to the nuclear ribosomal large subunit (nucLSU), the nuclear ribosomal intergenic spacers (nucITS, including the 5.8S rDNA), the mitochondrial ribosomal small subunit (mitSSU), and the largest subunit of the RNA polymerase II \textit{(RPB1)}. Other available gene loci were discarded due to insufficient data. Initial alignments were created with ClustalW (Thompson & al., 1994) and optimized manually using Seaview (Galtier & al., 1996). Mislabeled or otherwise unalignable sequences were removed during the process. Introns and ambiguously aligned regions were excluded prior to all analyses.

**Dataset assembly.** — The initial datasets for each locus were created by selecting from the initial alignments a maximum of two sequences per species. If more than two sequences were available for a given species, the longer sequences were given priority. As a consequence, the resulting single-locus datasets (1GENE, 762 OTUs) contained sequences from all species for which sequence information was available, but with no more than two OTUs per species. For a complete list of sequences see Appendix.

For the phylogenetic analysis of the combined data, three datasets were generated from the IGENE single locus datasets by combining only those specimens for which sequence data from at least two (2GENE, 433 OTUs), at least three (3GENE, 323 OTUs), or all four (4GENE, 145 OTUs) loci per specimen was present, following the strategy of Miadlikowska & al. (2006).

**Test for incongruence.** — The IGENE single locus data sets were used to test for topological incongruence among loci using the program compat3 (available at www.lutzonilab.net/downloads). For each locus individually, 500 bootstrap replicates (Felsenstein, 1985) were generated with RAxML v.7.0.4 (Stamatakis, 2006, Stamatakis & al., 2008) and all pairwise comparisons between the four loci were performed with compat3. A conflict between two loci was assumed when a clade was supported as monophyletic with a bootstrap frequency
≥75% in one tree, but supported as non-monophyletic in another (Mason-Gamer & Kellogg, 1996).

**Phylogenetic analyses.** — Phylogenetic searches were carried out by implementing maximum likelihood (ML) and Bayesian analyses on each of the three combined datasets (2GENE, 3GENE, and 4GENE). The analyses were run on the Duke Shared Cluster Resource (DSCR, Duke University, U.S.A.) and the computer cluster of the Nano+Bio Center (University of Kaiserslautern, Germany). If not stated otherwise, all three datasets were analyzed in the same way.

For one set of ML analyses the 2GENE, 3GENE and 4GENE combined datasets were partitioned into eight partitions: nuclLSU, mitSSU, nucITS1, nucl5.8S, nuclITS2, RPB1 1st position, RPB1 2nd position, and RPB1 3rd position. The ML analyses were carried out using RAxML v.7.0.4 (Stamatakis, 2006), implementing a GTR model of nucleotide substitution (Rodriguez & al., 1990) with a gamma shape distribution, and searching for the most likely tree with 500 heuristic replicates. Bootstrap frequencies (Felsenstein, 1985; Stamatakis & al., 2008) were estimated with 500 replicates.

The second set of ML analyses was implemented with GARLI v.0.96 (Zwickl, 2006). The 2GENE, 3GENE, and 4GENE datasets were analyzed unpartitioned, because GARLI currently does not support multiple partitions. Tree search was performed with 500 replicates using the standard settings of GARLI, implementing a GTR model of nucleotide substitution with a gamma shape distribution (approximated with four categories), and a proportion of invariable sites. Bootstrap frequencies were estimated with 500 replicates, limiting the parameter ‘genthreshfortopterm’ to 10,000 generations, as suggested in the manual.

In the Bayesian analyses the 2GENE, 3GENE, and 4GENE combined datasets were partitioned as described above. Modeltest (Posada & Crandall, 1998) was used to estimate for each dataset and each of the above partitions individually the number of substitution types, to test for an implementation of a gamma shape distribution (approximated with four categories) and to test for a proportion of invariable sites. Three independent runs with 30,000,000 generations, and four independent chains each were started with MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003) for each dataset, sampling every 500th tree. The temperature parameter for the (MC)
chains of MrBayes was lowered to 0.05 to ensure that a sufficient amount of state swapping occurred across the four chains. The burn-in fraction of sampled trees was estimated both by eye with ln-likelihood plots and using AWTY (Nylander & al., 2008).

Only nodes that received posterior probabilities equal and above 0.95 and ML-bootstrap support values equal or above 70% are interpreted as strongly supported.

### RESULTS

**DNA sequences and test for topological incongruence.** — A total of 201 new sequences were generated for this study, including 43 nucITS, 49 nuclLSU, 47 mitSSU, and 62 RPB1 sequences. The 1GENE-nucLSU dataset contained 353 taxa with a total of 3242 characters, 1357 of which could be unambiguously aligned. The 1GENE-nucITS dataset had 731 taxa and 533 characters, with 366 alignable positions. The 1GENE-mitSSU dataset contained 374 taxa with 2488 characters, 641 of which were unambiguous. The 1GENE-RPB1 dataset contained 205 taxa, and 615 of 760 characters could be unambiguously aligned. The test for topological incongruence (results not shown) displayed no supported conflicts at or above the generic level, and the single-gene datasets were thus combined for further analysis.

**Phylogenetic analyses.** — Analyses of three different datasets were performed: all OTUs with at least two loci (2GENE), at least three loci (3GENE), and a dataset only including OTUs with all four genes available (4GENE). There was no conflict (i.e., strongly supported conflicting topologies with ≥75% bootstrap support) between the phylogenetic trees obtained from these analyses and between ML and Bayesian analyses of each of the datasets. The trees obtained in the analyses on the 2GENE and 4GENE datasets are available as Figs. S1–S2, whereas the 3GENE dataset tree, being the best compromise between number of taxa and amount of missing loci, is shown in Fig. 1.

The combined 3GENE dataset contained 323 OTUs (311 nuclLSU, 315 nucITS, 307 mitSSU, 181 RPB1) and a total of 2970 characters, allowing for a maximum of one missing locus per OTU. After excluding alignment positions with only undetermined character states (positions containing only Ns, gaps, or missing data), the nuclLSU remained with 1351 unambiguous characters, and the mitSSU remained with 638 unambiguous characters. The total number of included characters for nucITS and RPB1 remained unchanged with 366 and 615 characters, respectively.

The optimal ML tree estimated with RAxML (ln likelihood = −44,695.13) is shown in Fig. 1. Because inferences from RAxML, GARLI and the Bayesian analysis presented no conflict, the ML tree obtained using RAxML is shown with support from the other two methods of analysis included. The three independent runs of MrBayes plateaued at different likelihood levels, and after discarding the first 15,000,000 generations as burn-in (50%), the last 30,000 trees of the best run were used to calculate the posterior probabilities for internal branches.

**Molecular phylogeny.** — A cartoon phylogeny that summarises all generic relationships within Parmeliaceae that are supported in at least one of the single-locus analyses is presented in Fig. 2. The core group of Parmeliaceae as circumscribed by Crespo & al. (2007) is monophyletic and strongly supported in the 4GENE dataset, but does not receive significant support in the 2GENE and 3GENE datasets. The sister-group relationship of Parmeliaceae in Parmeliaceae is not resolved with confidence, since the sister-group relationship with Usnea lacks support in all datasets analyzed. Monophyly of Parmeliaceae is strongly supported. Within Parmeliaceae, several well-supported major clades are distinguished. The Parmotrema clade includes the following monophyletic genera: Parmotrema (with two individuals of Canoparme- lia norstictica and one Parmelaria sp. nested within, and the C. crozalsiana group as sister to the remaining Parmotrema...
Fig. 1. Phylogram obtained from a ML analysis of the 3GENE dataset (see text for details), showing the phylogenetic relationships among Parmeliaceae. Continued overleaf.
Fig. 1. Continued.
spp), Flavoparmelia (with one Pseudoparmelia sp. nested within), Austroparmelia, Punctelia, Nesolechia, Flavopunctelia, and Canoparmelia s.str. The relationships among these lineages are strongly supported. The Xanthoparmelia clade is sister to the Parmotrema clade and this relationship is only supported in the Bayesian analysis. The former clade consists of a monophyletic genus Xanthoparmelia. The phylogenetic placement of the strongly supported, monophyletic genus Cetrelia is not recovered with confidence.

The Parmelina clade is strongly supported as monophyletic including the monophyletic genera Myelochroa and Parmelina, and in addition includes the monophyletic genus Remototrachyna and a paraphyletic Bulbothrix. In the 2GENE tree (Fig. S1), both specimens of Hypotrachyna radiculata compose a strongly supported lineage that is nested within Myelochroa. The strongly supported monophyletic Hypotrachyna clade includes the polyphyletic genera Everniastrum, Hypotrachyna, Parmelinopsis, and a monophyletic Cetrariastrum. In the 2GENE tree (Fig. S1), Cetrariastrum is nested within Everniastrum, but this relationship lacks support. The genera Parmelinopsis and the new genus Nipponoparmelia each form monophyletic groups with uncertain relationships. Relicina is strongly supported as monophyletic (including Relicinopsis in the 2GENE analysis, Fig. S1). The relationships of Relicina s.l., however, remain uncertain. Parmelia is polyphyletic, with one clade, segregated as Nipponoparmelia below with uncertain relationships, a clade of southern Hemisphere species (Parmelia spp. in Fig. 1) that is sister to Relicina, but without support, Parmelia masonii

**Fig. 2.** Cartoon tree summarizing our current knowledge of phylogenetic relationships within Parmeliaceae. Only relationships that received significant support in at least one of the analyses part of this study are shown. Numbers of species in each clade are in parentheses.
as sister to Melanelixia + Melanohalea, and Parmelia s.str. (Parmelia spp. in Fig. 1); Parmelia s.str. is strongly supported as monophyletic, but lacking support regarding intergeneric relationships. The Melanelixia and Melanohalea clades form one well supported clade in the 4GENE analysis (Fig. S2), but do not receive significant support in the 2GENE or 3GENE analyses (Fig. S1 and Fig. 1, resp.). Melanohalea is monophyletic and Melanelixia as well, with a strongly supported sister-group relationship to four species from the southern Hemisphere (previously placed in Melanelia) that are transferred to Melanelixia below. Three other Melanelia spp. (M. disjuncta, M. sorediata, M. tominii) cluster in one monophyletic group with Pleurosticta acetabulum.

The phylogeny of non-parmelioid Parmeliaceae is beyond the focus of this paper and will not be discussed in detail here. The well-supported relationships agree mostly with those discussed in Crespo & al. (2007), including strongly supported monophyly of alectoroid (Alectoria incl. Gowardia, Pseudephebe, Salcaria), cetarioid (Arctocetraria, Cetaria, Cetrelliopsis, Dactylina, Flavocetraria, Melanelia, Tuckermannopsis, Viápica), letharioid (Letharia, Lethariella), and psiloparmelioid lichens (Everniopsis, Psiloparmelia). Relationships among these groups and other monophyletic genera (e.g., Bryoria, Platismatia) remain largely unresolved. A more thorough taxon and gene sampling is needed to further assess phylogenetic relationships of these groups in Parmeliaceae.

A number of species in parmelioid lichens do not form monophyletic groups (e.g., Canoparmelia texana, Hypotrachyna revoluta, Melanelia disjuncta, Melanohalea exasperata, Parmelia tiliacea, Parmotrema reticulatum, Punctelia rudecta, Xanthoparmelia pulla; Fig. S1), indicating that additional studies are necessary to clarify their current delimitations, which are largely based on morphological and chemical characters.

**TAXONOMY**

Although there is a growing body of studies focused on certain groups of parmelioid lichens, ours is the first study addressing generic classification of parmelioid lichens as a whole using molecular data. Our analyses confirm previous studies that the generic classification is in need of further revision, with several genera being para- or polyphyletic. Here we present a new generic classification based on our phylogenetic studies and morphological and chemical evidence, listed alphabetically within major clades as indicated in Figs. 1 and 3. Each of the clades and genera are briefly characterized morphologically (Fig. 4), anatomically, and chemically. Taxonomic changes are only proposed for well-supported clades. A new genus, Emodomelanelia is described here, Nipponoparmelia is elevated to generic rank, and an additional 15 new combinations are proposed. The genus Parmelaria is reduced to synonymy with Parmotrema. We identify several groups for which additional taxon sampling and/or generation of molecular data are necessary for unequivocal resolution of their phylogenetic placement. Data on conidia were studied for the included species.

---

**Fig. 3.** Nine major groups within the parmelioid clade of Parmeliaceae sharing morphological and chemical characters. This is a cartoon tree summarizing our current knowledge of phylogenetic relationships based on nucITS, mitSSU, nucLSU, and RPB1 single-locus and combined datasets discussed in the text. Naming and numbering of the clades follows descriptions in the text. The size of the triangles and number behind the triangles indicate the number of species currently included in each of the clades. Branch lengths in this tree are uninformative. *The Parmelia clade is not supported in molecular analyses, but due to shared morphological and chemical characters we are treating the included taxa together in the text.

**1. Parmotrema clade**

This clade includes species that contain a not well characterized but diagnostic cell wall polysaccharide (isolichenan). Most species have a pored epicortex, some have pseudocyphelae, and they contain either atranorin or usnic acid as a cortical pigment (Fig. 4A–D). The center of diversity is in the Southern Hemisphere, with numerous tropical and subtropical species, some of which extend into temperate regions (Blanco & al., 2005, 2006).

Diagnostic characters. – Lobes subirregular; pored epicortex present; isolichenan; conidia cylindrical.

Notes. – The genus Austroparmelina was recently described (Crespo & al., 2010) for species previously placed in the polyphylectic genera Canoparmelia and Parmelia. This genus is sister to a clade comprising Flavoparmelia + Parmotrema. It differs from Parmotrema in having adnate thalli, narrow lobes, rhizines on the lower surface extending to the margins and cylindrical conidia; and from Flavoparmelia in having a grey upper cortex (containing atranorin). The monophyly of this genus and its relationships are well-supported. Crespo & al. (2007) showed that “Canoparmelia” prunata was not related to Canoparmelia s.str. Broadening taxon sampling to other species of Canoparmelia revealed (Fig. 1) that several species occurring in the Southern Hemisphere composed a novel clade in need of taxonomic recognition.


Diagnostic characters. – Lobes subirregular (Fig. 4A); pored epicortex present; isolichenan; conidia bifusiform.

Notes. – In its restricted circumscription, this genus includes species with broad and large ascospores, lacking depidiones and having a maculate upper surface. The genus in its restricted sense is a strongly supported monophyletic group whose common ancestry with the remaining genera within the Parmotrema clade is also strongly supported (Fig. 1). Molecular data suggest that Canoparmelia as originally circumscribed (Elix & al., 1986) is highly polyphylitic. Blanco and colleagues (Blanco & al., 2004b, 2005) showed that some Canoparmelia species clustered close to Parmotrema, and subsequently, Crespo & al. (2007) demonstrated that other Canoparmelia species were sister to Flavoparmelia and Parmotrema. These species were subsequently placed in the new genus Austroparmelina (Crespo & al., 2010). Here, we have found an additional species, Canoparmelia norsticticata, nested within Parmotrema (Fig. 1). This species is transferred to Parmotrema below, but the C. crozalsiana group that composes the sister lineage to Parmotrema requires additional study.


Diagnostic characters. – Broad lobes (Fig. 4B); pored epicortex present; isolichenan; conidia bifusiform; cortex with usnic acid.

Notes. – This genus was originally described as a segregate of Pseudoparmelia to accommodate species with broad lobes, containing usnic acid, isolichenan in cell walls, large ascospores and marginally erizinate lobes (Hale, 1986b; Elix, 1993). The phylogeny of Flavoparmelia is currently under study (Blanco pers. comm.). The genus is sister to Parmotrema from which it differs in having bifusiform conidia and always containing usnic acid. Our analyses suggest the placement of Pseudoparmelia subambigua within Flavoparmelia and consequently it is here transferred to this genus.


Diagnostic characters. – Lobes subirregular; non-pored epicortex, with punctiform pseudocyphellae; isolichenan; conidia bifusiform; containing usnic acid.

Notes. – This genus was originally described as a subgenus of Punctelia (Krog, 1982), but was later raised to generic level (Hale, 1984a) based on differences in conidial morphology. Molecular studies confirm the distinction of these two groups with roundish pseudocyphellae at generic level. This small genus (7 species) occurs in temperate and tropical regions on all continents except Australia.


Diagnostic characters. – Lichenicolous fungus; gall forming; thallus endokapylic; apothecia with entire margin; conidia bacilliform.

Notes. – The genus Nesolechia was treated as a synonym of Phacopsis Tul. by Triebel & Rambold (1988) based on the absence of great anatomical differences between both genera. This was not accepted by some authors and Alstrup & Haswkwsworth (1990) offered several characters in which both genera differ. Subsequently, Diederich (2003) supported congenerity based on similarities of epitheinal and hypothecial pigments. The molecular study of species of Phacopsis and Nesolechia by Peršoh & Rambold (2002) revealed their placement in Parmeliaceae for the first time, later supported by Crespo & al. (2007). However results in Peršoh & Rambold (2002) revealed the polyphyly of the genus Phacopsis. Thus, until further research is made in this group we propose to keep the name Nesolechia. In our analysis specimens of Nesolechia represent the sister group to the genus Punctelia; this relationship is well-supported in all the trees generated.


= Canomaculina Elix & Hale in Mycotaxon 29: 239. 1987 – Type: C. pilosa (Stizenb.) Elix & Hale in Mycotaxon 29:
Generic classification of parmelioid lichens


Diagnostic characters. – Broad lobes (Fig. 4C); pored epicortex present; intermediate-type lichenan between Cetraria-type and Xanthoparmelia-type lichenan; conidia cylindrical.

Notes. – The genus as now circumscribed includes ca. 350 species that have their center of distribution in tropical regions and consequently the two species that have cell wall polysaccharides with Xanthoparmelia-type lichenan. Most species occur in the Southern Hemisphere in arid or semiarid subtropical areas, with some extending into temperate regions. The species in this clade lack true pseudocyphellae, have a pored epicortex (Fig. 4E), and show a considerable variation in cortical chemistry, including species containing usnic acid, atranorin or lacking cortical phenols (Blanco et al., 2004b; 2006).


Diagnostic characters. – Pored epicortex present; Xanthoparmelia-type lichenan; conidia bifusiform or cylindrical; ascospores arachiform.

Notes. – The genus Xanthoparmelia was the subject of several recent phylogenetic studies, resulting in a merging of a
number of previously recognized genera within it (Blanco & al., 2004b; Thell & al., 2006; Amo & al., 2010a,b); the most recent being Karowia, Omphalodiella and Placoparmelia (Amo & al., 2010a,b). The clade is well-supported as monophyletic, but the absence of distinct morphological traits associated with well-supported monophyletic groups within the Xanthoparmelia clade prevents the recognition of smaller genera within this large genus. Morphological variation within this clade is likely to be driven by environmental factors and were overemphasized in previous classifications (Lumbsch & al., 2008).

3. Cetrelia clade

This clade consists only of the genus Cetrelia, which was traditionally regarded as cetrarioid based on the presence of marginal apothecia, but is now considered to belong to parmelioid lichens based on inferences from molecular data (Crespo & al., 2007). The genus has broadly lobed thalli and was previously regarded as a “parmelioid Cetraria” (Culberson & Culberson, 1968). Furthermore, Cetrelia has isolichenan as cell wall polysaccharide (Elix, 1993), which occurs in several groups of parmelioid genera, but is absent in the cetrarioid cell wall polysaccharide (Elix, 1993), which occurs in several groups of parmelioid genera, but is absent in the cetrarioid clade. This clade is enlarged from its previous concept (Delise) W.L. Culb. & C.F. Culb. in Contr. U.S. Natl. Herb. 34: 498. 1968 (Type: Parmelia perlat a var. cetrarioidea Delise in Duby, Bot. Gall. Pars Secunda: 601. 1830).

Diagnostic characters. – Broad lobes (Fig. 4F); non-pored epicortex, punctiform pseudocyphellae present; isolichenan; conidia bifusiform; apothecia marginal.

4. Parmelina clade

The Parmelina clade is enlarged from its previous concept (Blanco & al., 2006) to include Bulbothrix, Parmelinella and Remototrachyna in agreement with Divakar & al. (2010) as well as Myelochroa and Parmelina. The latter three genera were previously placed in the Hypotrachyna clade, but the relationships of these genera within the Hypotrachyna clade, in a restricted sense, lacked support. Species in the Parmelina clade have isolichenan in the cell walls, a pored epicortex, lack pseudocyphellae, and contain atranorin or usnic acid as cortical compounds (Fig. 4G–I).


Diagnostic characters. – Lobes subirregular (Fig. 4G); conidia cylindrical or bifusiform; bulbate cilia present.

Notes. – The circumscription of this genus remains uncertain. In current phylogenies, the genus is paraphyletic. We have so far not been able to get sequences of the species that includes the type of the name and our taxon sampling is still poor. Additional data are required to address the issue of monophyly and circumscription of Bulbothrix.


Diagnostic characters. – Lobes subirregular (Fig. 4H); conidia cylindrical or bifusiform; yellow-orange medulla (secalonic acid derivatives).

Notes. – This relatively small genus (ca. 30 species) has its center of distribution in eastern Asia and is characterized by the presence of yellow-orange pigments (secalonic acid derivatives) in the medulla and simple to squarrosely branched rhizines. It is morphologically similar to Parmelina, which is also sister to it, but the latter differs in having a white medulla and lacking hophane triterpenes. Interestingly, these two clades have a largely vicariant distribution: while Myelochroa is chiefly distributed in eastern Asia, Parmelina is largely confined to winter-rain areas in the west of Europe and North America and adjacent regions. The status of the two genera merits further study. Results from Divakar & al. (2006) show the phylogenetic placement of Hypotrachyna radiculata within Myelochroa. Consequently, it is here transferred to this genus.


Diagnostic characters. – Lobes subirregular (Fig. 4I); conidia cylindrical; medulla white; upper part of inner excipulum carbonized.

Notes. – When originally described, the genus Parmelina (Hale, 1974) included a number of unrelated elements that were subsequently placed elsewhere (Elix & Hale, 1987; Crespo & al., 2010). In its restricted sense, the genus is confined to the Northern Hemisphere with a center of distribution in western North America and Europe. In apothecial sections a thin carbonized layer is seen in the upper part of the inner excipulum, corresponding to an amphithecial ring seen in a superficial view of the ascomata. The closest relative, Myelochroa, is mainly distinguished from it based on chemical characters.


Diagnostic characters. – Lobes subirregular; conidia cylindrical or bifusiform; bulbate cilia absent; yellow-grey upper cortex (secalonic acid derivatives).

Notes. – Parmelinella is nested within a clade of Bulbothrix and its generic status is in need of revision. A study addressing the generic concept in the Bulbothrix/Parmelinella group
requires more thorough taxon sampling. Under the current
generic circumscription, this small genus of three species is
distinguished from Bulbothrix mainly by the absence of bulbate
cilia and the presence of secalonic acid derivatives, characters
that are not supported as taxonomically important in molecular
phylogenies of parmelioid lichens (Divakar & al., 2006).

2010 – Type: R. flexilis (Kurok.) Divakar & A. Crespo in
Amer. J. Bot. 97: 586. 2010 (Parmelia flexilis Kurok. in

Diagnostic characters. – Lobes broad; conidia bifusiform;
outer exciple with very thick cell walls.

Notes. – This recently described genus (Divakar & al.,
2010) was previously included in Hypotrachyna, but is not
closely related to that genus, from which it differs in lobe mor-
phology, rhizine length, hymenium height, exciple structure,
and ascospore size. Remototrachyna is distinguished from
Bulbothrix by having broader lobes, lacking bulbate cilia, a
higher hymenium, and larger ascospores. Remototrachyna has
its center of distribution in Southeast Asia.

5. Hypotrachyna clade

This clade includes the genera Cetrariastrum, Evernias-
strum, Hypotrachyna, and Parmelinopsis. All have isolichenan
as cell wall polysaccharide. They are currently poorly known
and have their center of species diversity in the tropical and
subtropical regions of both Hemispheres. All taxa in this clade
have a pored epiderm and lack secalonic phellae (Fig. 4J–L).
They may contain atranorin, usnic acid or lichexanthone as
cortical substances. Some of the genera in this clade are not
monophyletic. However, since the backbone of the phylogeny
within the group is lacking support, we refrain from drawing
nomenclatural conclusions before additional data become avail-
able.


Diagnostic characters. – Lobes linearly elongate; conidia
cylindrical; apothecia with solid stipe.

Notes. – This genus was separated from Everniastrum,
which differs in having more regularly branched lobes, a hol-
low stipe, larger asci and a thinner hypothecium (Sipman,
1980, 1986). However, the distinction between the two genera
is disputed (Culberson & Culberson, 1981). Additional data are
necessary to clarify their taxonomic status.

Everniastrum Hale ex Sipman in Mycotaxon 26: 237. 1986 –
Type: E. cirrhatum (Fr.) Hale ex Sipman in Mycotaxon
26: 237. 1986 (Parmelia cirrhata Fr., Syst. Orb. Veg. 1:
283. 1825).

Diagnostic characters. – Lobes linearly elongate (Fig. 4J);
conidia bifusiform; apothecia with hollow stipe.

Notes. – The distinction of this genus from Cetrariastrum
requires further studies, as discussed above. This is a pantro-
pical genus with centers of distribution in the Neotropics
and Asia.

Hypotrachyna (Vain.) Hale in Phytophyla 28: 340. 1974 – Type:
H. brasiliiana (Nyl.) Hale in Phytophyla 28: 340. 1974 (Par-
meila brasiliiana Nyl in Flora 68: 611. 1885).

Diagnostic characters. – Lobes dichotomously branched,
with truncate apices (Fig. 4K); conidia bifusiform; rhizines
richly dichotomously branched.

Notes. – This pantropical genus is paraphyletic in its cur-
rent circumscription. Asian species with broad lobes were
shown to be unrelated and consequently separated as Remoto-
trachyna (Divakar & al., 2010). The classification of the re-
mainig Hypotrachyna species needs to be addressed by a
study including more taxa and molecular characters.

Parmelinopsis Elix & Hale in Mycotaxon 29: 242. 1987 – Type:
1987 (Parmelia horrescens Taylor in Mackay, Fl. Hibern,
Part 2: 144. 1836).

Diagnostic characters. – Lobes dichotomously branched,
with truncate apices (Fig. 4L); conidia bifusiform or cylindri-
cal; rhizines simple to sparsely dichotomously branched.

Notes. – This pantropical to temperate genus is paraphyle-
etic and nested within Hypotrachyna. Traditionally it has been
distinguished from Hypotrachyna based on the presence of
cilia and less richly branched rhizines. It remains to be seen
whether this genus can be kept separate from Hypotrachyna in
a modified circumscription or needs to be synonymized with
Hypotrachyna.

6. Parmeliopsis clade

This small clade includes only the genus Parmeliopsis, a
genus of six species. The phylogenetic placement of this clade
remains uncertain. It is unique among Parmeliopsis for having
richly branched conidiophores (Vobis, 1980).

Lich. 2: 54. 1869 (Lichen ambiguaus Wulfen in Jacquin,
Collectanea 4: 239. 1790).

Diagnostic characters. – Lobes subirregular; pored epi-
cortex present; isolichenan; conidiophores branched; conidia
falcate.

7. Nipponoparmelia clade

This newly discovered clade includes a group of East
Asian species previously placed in Parmelia s.str. (Hale,
1987) that differs morphologically from other species in this
genus by having lateral, punctate pseudocyphellae. It was
later treated as a subgenus Nipponoparmelia within Parmelia
(Kurokawa, 1994). The subgenus is here raised to the generic
rank.

*Diagnostic characters.* – Lobes subirregular; non-pored epicortex, punctiform pseudocyphellae present; conidial cylindrical.  
*Notes.* – This small East Asian genus is characterized by marginal punctiform pseudocyphellae, grey to grey-brown thalli and simple to furcate rhizines. The following four species are included in the current circumscription of this genus.


**Nipponoparmelia ricasolioides** (Nyl.) A. Crespo & Divakar, **comb. nov.** [MB MB516762] ≡ *Parmelia ricasolioides* Nyl. in Flora 70: 135. 1887.

### 8. *Parmelia* clade

This group is not strongly supported as monophyletic but additional data are required to evaluate the relationships of the genera listed here. Morphologically these genera are diverse and also include biogeographically distant entities, such as the primarily northern hemispheric, temperate genus *Parmelia* and the tropical genera *Relicina* and *Relicinopsis*.


*Diagnostic characters.* – Lobes subirregular (Fig. 4M); non-pored epicortex, effigurate to elongate pseudocyphellae present; isolichenan; conidial cylindrical or bifusiform.  
*Notes.* – Among the most surprising result of our analyses was the polyphyly of *Parmelia* s.str. A group of East Asian taxa with punctiform pseudocyphellae is segregated as *Nipponoparmelia* (see above), whereas a predominantly Australasian group of species related to *P. signifera* is tentatively kept in *Parmelia*. However, relationships among these well-supported groups are resolved only with short internodes, none of which well-supported. This predominantly Australasian clade includes species with usually broader lobes, but additional morphological studies are needed in addition to a more extensive taxon sampling and molecular characters, to better understand the phylogeny of this clade. *Parmelia* in its restricted sense is a small genus of temperate species, with a center of distribution in the Northern Hemisphere.


*Diagnostic characters.* – Lobes sublinear, subdichotomously to dichotomously branched; pored epicortex present; isolichenan; conidial bifusiform; cortex with usnic acid; bulbate cilia present.  
*Notes.* – This tropical genus has its center of species diversity in eastern Asia and Australasia. It is similar to *Bulbothrix* in having bulbate cilia, but differs from that genus in cortical chemistry and conidia shape and is not closely related. Another similar genus is *Relicinopsis*, which primarily differs in lacking bulbate cilia and having fusiform conidia. Our studies indicate that the two genera are probably better regarded as synonymous, since *Relicinopsis* is nested within *Relicina* in the IGENE analysis. However, this relationship lacks support and hence additional data are required before any nomenclatural conclusion is reached.


*Diagnostic characters.* – Lobes sublinear, subdichotomously to dichotomously branched; pored epicortex present; isolichenan; conidial elongate fusiform or cylindrical; cortex with usnic acid; simple cilia present.  
*Notes.* – The taxonomic status of this genus remains uncertain, see under *Relicina*.

### 9. *Melanohalea* clade

This clade is expanded in comparison with its previous circumscription (Blanco & al., 2006) to include also the *Melanelia* clade. Genera in this clade have a cell wall polysaccharide that has not yet been identified and may or may not have a pored epicortex and/or pseudocyphellae. Neither atranorin nor usnic acid is present as cortical compounds, but species in this group contain melanoid substances that are responsible for their brown color (Fig. 4N–O). The *Melanelia disjuncta* group has not yet been assigned to a genus. The group certainly is not related to *M. stygia*; the type of *Melanelia*, which is a cetrariaoid genus. However, additional data are necessary to evaluate whether this group can be placed within one of the current genera in the *Melanohalea* clade or whether a new genus needs to be described to accommodate these taxa.

Thallus laxe adnatus, pallide ad obscure brunneus; cum pseudocyphellis marginalibus vel etiam laminalibus, albis; soralia isidiaque desunt; superficies inferior nigra; cum rhizinis simplicibus vel furcatis, nigris. Apothecia sessilia vel substipitata, cum marginibus pseudocyphellatis; ascosporae parietibus ca. 1–2 μm crassis, Conidia bifusiformia.

Diagnostic characters. – Thallus olive brown to brown; lobes narrow to moderately broad; non-pored epicortex, effigurate pseudocyphellae present; conidia bifusiform; cortex HNO₃+ green.

Etymology. – The epithet emodo refers to the Himalayas and melanella to brown color of the thallus upper surface.

Notes. – This new monospecific genus includes a Parmeliaoid species that combines characters typical for Parmelia s.str., such as laminal and marginal effigurate pseudocyphellae and large ascospores, with characters typical of the brown Parmeliaoid genera, such as an olive brown to brown upper surface and lack of atranorin. When describing the new species, Esslinger & Poelt (1991) pointed out that the placement in that genus was tentative. The species is an Asian endemic, known from mainland China, India, Nepal and Taiwan, where it is common on rocks in subalpine to alpine habitats (Esslinger & Poelt, 1991; Ahti & al., 1999; Kurokawa & Lai, 2001; Divakar & Upreti, 2005b).


Diagnostic characters. – Lobes subirregular, plane to concave (Fig. 4 N); pseudocyphellae present, on tubercula; conidia elongate cylindrical to fusiform; cortex HNO₃+.

Notes. – This genus is most common in the Northern Hemisphere and includes species occurring on bark or wood. It is characterized by pseudocyphellae, often on warts or isidial tips, a nonpored epicortex, and a medulla containing depsidones or lacking secondary compounds.


Diagnostic characters. – Broad lobes (Fig. 4O); pored epicortex present; isolichenan; conidia cylindrical to elongate fusiform; cortex HNO₃+ violet.

Notes. – This is a small genus of two species that is restricted to Eurasia and North Africa. Its relationships with other groups of brown Parmelioid lichens requires further study.

Excluded genera and genera not studied

The following genera formerly placed in the Parmelioid group based on morphology (Elix, 1993; DePriest, 1999) belong to other non-parmelioid groups: Allantoparmelia (Vain.) Essl., Arctoparmelia Hale, Evertipopsis Nyl., Imshaugia S.L.F. Mey., Melanelia Essl., Omphalodium Meyen & Flot., Omphalora T.H. Nash & Hofeller, and Psiloparmelia Hale. Evertipopsis and Psiloparmelia were previously shown to belong to a separate psiloparmelioid group within Parmeliaceae (Crespo & al., 2007), while numerous studies have shown that Melanelia s.str. belongs to the clade of cetrarioid lichens (Blanco & al., 2004a, 2006; Thell & al., 2004, 2009; Crespo & al., 2007). The placements of Allantoparmelia and Imshaugia within Parmeliaceae remain uncertain (Thell & al., 2004; Crespo & al., 2007), while Arctoparmelia has been shown to belong to the hypogymnioid group (Crespo & al., 2007). Omphalodium and Omphalora originated outside the Parmelioid group (Thell & al., 2002, 2004).

The species that include the types of the following generic names have not yet been studied by molecular methods.
and hence their placement and taxonomic status is unknown: Bulborrhizina Kurok., Parmotremsis Elix & Hale, and Pseudoparmelia.

**DISCUSSION**

In this study we have gathered DNA sequence data available in GenBank and obtained 201 new sequences to address the generic circumscriptions in all clades of parmelioid genera. Our analyses identified eight well-supported major clades within parmelioid lichens, the majority agreeing with the clades found by Blanco & al. (2006). The exceptions include an enlarged circumscription of the Parmelina clade to include taxa previously placed in the Hypotrachyna clade and inclusion of the Melanelia clade in the enlarged Melanohalea clade. The Cetrelia, Nipponoparmelia, Parmeliopsis clades are here newly recognized. We attempted to keep nomenclatural changes at a minimum. Although four clades were shown to be independent and merit recognition at some taxonomic level, we only proposed the acceptance of two new genera. One new genus (Emodomelanella) is described and a new combination into Nipponoparmelia is made for species previously classified in the highly polyphyletic genus Parmelia sensu Hale (1987). Even after segregation of these two genera, Parmelia remains highly polyphyletic. The Canoparmelia crozalitana and Parmelia signifera groups are shown to be unrelated to the species that include the types of their generic names. However, we refrain from describing new genera for those groups here, since our understanding of the morphological characters to circumscribe these clades is currently too poor. Additional taxonomic studies are necessary before nomenclatural changes are made.

We also identified a number of remaining problems in the generic classification of parmelioid lichens. These include the circumscription of Parmotrema (especially the relationships to the Canoparmelia crozalitana group), the segregation of Bulbothrix into two clades with Parmelinella nested within one of these clades, the distinction of Myelochroa and Parmelina, the generic circumscription in the Hypotrachyna clade (i.e., the polyphylety of Everniastrum, Hypotrachyna and Parmelinopsis), polyphyly of Parmelia (with the Australasian P. signifera probably representing a distinct lineage), the relationships of Relicina and Relicilcopsis, and the placement of the Melanelia disjuncta group. Further, no molecular data are available for the species that include the types of three generic names (Bulborrhizina, Parmotremsis, Pseudoparmelia). Thus, our study has effectively focused forthcoming generic level phylogenetic studies in this lichen group on these problematic generic groups.

Although a number of problems remain, significant progress in our understanding of the phylogeny of parmelioid lichens has been made during the last decade. The classification of the family has now been put on a sound phylogenetic basis. A few new genera have been described, while many others have been synonymized. The taxonomic significance of morphological and chemical characters at the generic level was evaluated. Some vegetative characters, such as the presence of cilia and rhizine-types, are shown to be too homoplasious and hence of minor importance at the generic level for parmelioid lichens. More changes in the generic classification will ensue following additional studies directed at the problems identified here. Further, a major remaining problem is to resolve the backbone relationships among major clades of parmelioid lichens, which will require the sequencing of additional loci. However, a stable framework for the generic classification has been developed in this collaborative project. We hope that this framework will assist lichenologists in the near future to refine a generic classification of parmelioid lichens that reflects the phylogenetic relationships.

**ACKNOWLEDGEMENTS**

We wish to thank Allison Knight, Gary Perlmutter, Ken Sweat, James Lendemer and Gennadii Urbanavichius for providing us with fresh material for our studies. We thank John Pormann and Sean Dilda from the Duke Shared Cluster Resource and Michael Nuhn from the Nano-Bio Center for their support with installing and running the necessary software. This study has been supported financially by the Spanish Ministerio de Ciencia e Innovación (CGL2008-01125/E/ BOS, CGL2007-64652/BOS), and Ramon y Cajal grant (RYC02007-01576) to PKD, a start up fund of The Field Museum to Thorsten Lumbsch, the Swedish Research Council grants VR 629-2001-5756, VR 621-2003-303 and VR 621-2006-3760 to Mats Wedin. We thank the Galapagos National Park for permission to analyze their material. This is publication no. 2001 of the Charles Darwin Research Station.

**LITERATURE CITED**


Lumbsch, H.T., Hipp, A.L., Divakar, P.K., Blanco, O. & Crespo, A.


