

Generic concepts in parmelioid lichens, and the phylogenetic value of characters used in their circumscription

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Abstract: This article traces the changing systems in the classification of the parmelioid lichens from the early 19th century to the present day. Molecular phylogenetic approaches have enabled the relative importance of traditionally used characters to be objectively re-assessed, and led to the realization of the significance of others that had previously been passed over or dismissed; for example, differences in ascospore and conidium types or the cell-wall constituents. Information on the different characters employed is presented and assessed. It is concluded that characters related to thallus form or chemical products prove to be less informative at the generic level than has sometimes been assumed. Features requiring further study are identified, and in the light of experience in this group, lichenologists should be cautious in translating their results into formal taxonomies.

Key words: chemotaxonomy, Lecanoromycetes, molecular systematics, *Parmeliaceae*, taxonomy

Introduction

Nothing is more irritating to those who use the scientific names of organisms than to find those names have changed (Nimis 1998). This irritation is especially acute when there is a seemingly constant flux of advice as to what is or what is not to be employed. The feeling of frustration is often accentuated by the reasons for the change not being either explained or understood. Instability in scientific names results from either a combination of nomenclatural nuances, or new scientific data or opinions, or sometimes both. These problems are particularly acute in groups of organisms which include numerous species and also have not been subject to intensive research into their evolutionary history. It is pertinent to reflect that a scientific name is essentially a scientific hypothesis. The name is a statement that here is an organism (or group of organisms) with a particular

circumscription and rank which should be classified in a particular way because of its relationships. And, as with any hypothesis, the concept represented by the name is open to testing.

Over the course of the last forty years in particular, the instability of names at the generic level has become notorious in the parmelioid lichens (i.e. most of the foliose representatives of the *Parmeliaceae*). The objective of this contribution is to explain the reasons for the changing concepts, and the progress made towards a phylogenetically robust and generally accepted system made during the last ten years.

Changing generic concepts

The generic concepts employed for lichen-forming fungi have evolved as a consequence of new understandings and new technologies, from the advent of light microscopes through the analysis of chemical products to scanning electron microscopy, cladistics, and now molecular phylogenetics. An overview of changing generic concepts in the pre-molecular age is provided by Hale

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(1984*a*), who noted that many genera introduced in the mid-1800s and then ignored were being reinstated. DePriest (1999) explored the work of Hale and his contemporaries in some detail, and also tabulated lists of genera accepted in various works. However, an explanatory account, tracking the changing generic concepts in the parmelioid lichens from the first use of *Parmelia* by Acharius (1803) to the present day, does not seem to have been produced. Now that an international consensus has emerged (Crespo *et al.* 2010*a*), it is timely to explain the situation to lichenologists as a whole and place it in a historical perspective¹.

1803–1850

The generic name *Parmelia* was introduced by Acharius (1803: xxxiii) for lichens in a group including ones which had open rounded apothecia with a “margin thallo concolori”, and distinguished from *Urceolaria* by the apothecia being raised above the thallus surface rather than immersed. He did not take up *Lichen* sect. *Imbricaria*, which he had used earlier infragenerically (Acharius 1798: 107), for such foliose lichens, as that name was already in use in plants². The genus included 204 species, the thalli of which were “polymorphus”, and this first circumscription included lichens with leprose and crustose thalli (e.g. *Caloplaca cerina* group, *Rinodina*, *Tephromela*, *Trapelia*) as well as macrolichens no longer regarded as parmelioid (e.g. *Alectoria*, *Anaptychia*, *Collema*, *Lobaria*, *Physcia*, *Ramalina*, *Teloschistes*). Subsequently, Acharius (*in* Luyken

1809: 91) restricted *Parmelia* to lichens with centrally fixed apothecia and foliose stellate to strap-like thalli. Sixty species were accepted in Acharius (1810), including, in addition to ones now regarded as parmelioid, species now placed in genera as diverse as *Degelia*, *Pannaria*, *Physcia*, *Physconia*, and *Xanthoria*.

1851–1919

Acharius' concept of the genus was generally adopted until the importance of ascospores in ascomycete classification started to be appreciated in the 1840s. The discovery that the ascospores differed in colour and/or septation in some *Parmelia* species quickly led to this segregation to re-circumscribed genera such as *Physcia*, or newly described ones such as *Xanthoria*. The application of names did, however, vary; for example Körber (1855) adopted *Parmelia* for foliose species with 1-septate brown spores (i.e. *Anaptychia* and *Physcia* in the modern sense), *Imbricaria* for those with 0-septate colourless spores (i.e. parmelioid lichens in the modern sense), and *Physcia* for ones with polarilocular colourless spores (i.e. *Xanthoria* species). However, *Parmelia* soon came to be accepted for species with simple colourless spores (e.g. Nylander 1855; Fries 1861). Massalongo (1854) segregated *Menegazzia* primarily because of the very large thick-walled spores and later *Parmotrema* because of the perforated apothecia (Massalongo 1860).

Nylander (1860) stressed the colourless non-septate spores in his circumscription, accepting 46 species worldwide and arranging them into eight groups, many of which were later to be recognized as separate genera. However, Nylander appears never to have recognized Massalongo's two segregates, but he did introduce two novelties: *Parmeliopsis* separated by the conidium type as a subgenus name in 1861, raising it to generic rank in 1866; and later *Hypogymnia* with an inflated non-rhizinate thallus as a subgenus in 1881.

Vainio (1890), wrestling with the huge diversity of parmelioid lichens he encountered in Brazil, was the first author to strive to

¹ Only works that relate to changing generic concepts are cited in this section, not regional or world monographs of particular genera or revisions of particular species complexes. DePriest (1999) includes references to many such works that appeared in the period 1958–95.

² *Imbricaria* Juss. 1789 (*Sapotaceae*) and *Imbricaria* Sm. 1797 (*Myrtaceae*). *Imbricaria* was used at the generic level in lichens by Michaux (1803: 322) who attributed it to “Ach.”, but Acharius had used it only within the generic name *Lichen* and seems to have taken the name from Schreber (1791) whose work he mentions (e.g. p. 112) although not just where the sectional name was used.

distinguish groups of species within the genus. He recognized three sections: *Amphigymnia* (broad and ascending lobes, often a broad zone without rhizines below, and also often cilia on the margins; with subsections *Subglaucescens* with grey or white thalli, and *Subflavescens* with yellowish thalli), *Hypotrachyna* (elongated lobes and minute rhizines; with subsections *Cyclocheila* with adpressed lobes and hardly raised apothecia, *Irregularis* with irregular broad lobes and raised apothecia, and *Sublinearis* with adpressed di- or trichotomous lobes and commonly sessile apothecia), and *Xanthoparmelia* (yellowish, adpressed, with elongated lobes; with subsections *Endoleuca* with a white medulla, and *Endoxantha* with a yellow medulla).

Independently, in cataloguing 380 species Nylander had under *Parmelia* amongst his “exotic” lichens, Hue (1892) confronted similar problems to Vainio, but on an ever grander scale. He recognized four subgenera, *Anzia*, *Hypogymnia*, *Omphalodium* and *Parmelia*, but divided the last into 12 “stirps”, several of which were destined to be treated as separate genera by future workers (e.g. stirps *Parmeliae borrieri*, *Parmeliae caperatae*, *Parmeliae conspersae*, *Parmeliae olivaceae*, *Parmeliae relicinae*, *Parmeliae saxatilis*, *Parmeliae stygiae*, *Parmeliae tiliaceae*). However, no diagnoses were provided for these “stirps”. Hue subsequently recognized sections *Everniiformes* and *Melaenoparmeliae* (Hue 1899). It is evident that Hue had a deeper appreciation of groupings within the genus than his predecessors and contemporaries, something that appears not to have been previously noted.

The first group of parmelioid lichens to be monographed in detail, with photographs and full descriptions, was subgenus *Hypogymnia* studied by Bitter (1901). He set a standard scarcely to be emulated again until the 1970s, and dispersed the species through two sections, *Solidae* and *Tubulosae*, distinguished by a solid and hollow medulla respectively. Around this time, Zopf (1903) introduced the generic name *Pseudevernia* for *Parmelia furfuracea* and some newly recognized, including chemically separated, species but this was not taken up until the

1950s and the species continued to languish in *Everniaeformes*.

Another critical study, this time of 14 brown species, was carried out by Rosendahl (1907) who carefully studied anatomical features and compared them with some grey species, including *Parmelia sulcata* and *Pseudevernia furfuracea*; he noted differences in cortical structure and also found ascospore size to have value, at least as a specific criterion.

Zahlbruckner (1908), in an overview of the accepted genera of lichens worldwide, largely followed Vainio and Bitter, and recognized five subgenera within *Parmelia*: *Euparmelia* (with sections *Everniaeformes*, *Melaenoparmelia*, *Xanthoparmelia* with subsections *Endoleuca* and *Endoxantha*, *Hypotrachyna* with subsections *Sublinearis*, *Cyclocheila* and *Irregularis*, and *Amphigymnia* with subsections *Subflavescentes* and *Subglaucescens*), *Hypogymnia* (with sections *Tubulosae* and *Solidae*), *Menegazzia*, and *Omphalodium*. *Anzia* (including section *Pannoparmelia*) and *Parmeliopsis* (including section *Chondropsis*) were treated as separate genera. Bitter’s *Hypogymnia* sect. *Solidae* was raised to subgeneric rank as subgenus *Allantoparmelia* by Vainio (1909) for the solid-lobed species of *Hypogymnia*, characterized by brown, narrowly lobed adpressed thalli lacking rhizines.

Dealing only with the French species, Harmand (1909) differed in retaining *Parmeliopsis* as a subgenus and, interestingly, included *Parmelia loxodes* in sect. *Xanthoparmelia*, although this may have been inadvertent rather than prescient as it appears he saw no specimen. An interesting innovation was, however, the introduction of an additional subsection within sect. *Amphigymnia*: *Olivascentes* for *P. acetabulum*.

Lynge (1914) revised the South American *Parmeliaceae* from the Regnell expedition, in which 39 of 76 species (i.e. 51 %) were described as new to science; again demonstrating the richness of the group in the tropics. He described *Pseudoparmelia* as a separate genus based on a single specimen in which the lower cortex lacked rhizines. Within *Parmelia* itself, he followed Vainio’s scheme, but interpolating a new section

Bicornuta for a single species with apically attenuated ascospores, *P. semilunata*.

1920–1959

In his studies of lichens in the Philippine Islands, Vainio (1923) replaced section *Hypotrachyna* with two sections he had previously recognized as subsections, sections *Irregularis* and *Sublinearis*, but did not provide an overall revision of his system. Du Rietz (1924) was not content with Vainio's scheme, however, and introduced a new sectional name *Reticulatae* for sect. *Irregularis* and some additional species; his name is consequently superfluous and needs to be rejected.

Nevertheless, Zahlbruckner (1926) did not modify his scheme from 1908, apart from the recognition of *Pseudoparmelia* as a genus separate from *Parmelia*; the type species of subgenus *Allantoparmelia* (i.e. *P. alpicola*) was retained in subgenus *Hypogymnia*, and Vainio's name was treated as a synonym in the *Catalogus Lichenum Universalis* (Zahlbruckner 1929). The *Catalogus* was a remarkable achievement, especially for a single person, and in it 629 species were accepted in *Parmelia* with full details of places of publication, synonyms and chresonyms³.

Surprising as it may appear, the concept of fixing the application of scientific names by name-bearing types entered biological nomenclature rather late. The idea was proposed by American botanists in 1904, but not accepted at the subsequent International Botanical Congress in Vienna in 1905; this contributed to the break-away American Code of Botanical Nomenclature. It was not until the 5th International Botanical Congress in Cambridge in 1930 that the idea was accepted, and this did not become a requirement until 1958 (Perry 1991). Following the American trend, and the 1930 decision, in the case of fungal genera, including those that form lichens, the Americans Clements & Shear (1931) listed type species for both accepted genera and synonyms, many

selected by them from "the best known or more important species generally included in the genus at present". This is relevant here, as they understandably chose *Parmelia conspersa* as the type species of *Parmelia*, which was also one of the original species included in the genus by Acharius (1803).

Almost all lichenologists were content to follow the system in Zahlbruckner's *Catalogus*, with one notable exception: the Hungarian lichenologist, and for a short time Minister of Culture and Education, Köfaragó-Gyelnik. He was generally viewed as something of a nomenclatural terrorist by his contemporaries who were infuriated by the large numbers of novel taxa he described, most of which they could not accept, and an apparent slackness in how he worked (Sjödín 1954). However, as pointed out by Hale (1990), "he had a far deeper, though sometimes garbled, understanding of *Xanthoparmelia* – and other genera – than any other lichenologist of his day and was clearly far ahead of his time", for example in his widespread use of chemical reagent tests. Gyelnik (1932) elaborated his own system for the European parmelioid lichens with a series of subgenera, sections and subsections (Table 1). He stressed ascospore type and the presence of rhizines as subgeneric characters, thallus form and colour at the subgeneric level, and surface features, medulla colour and cilia at the subsectional level. Many of these characters were later to be utilized at the generic level in the 1970s and 1980s.

Hillmann (1936) was very conservative in his treatment of the central European parmelioid lichens, essentially following Zahlbruckner's system of subgenera and sections, apart from a new subsection *Soraliferae* within subgenus *Hypogymnia* for the *P. physodes* group, to differentiate them from the diffuse-sorediate species. He also introduced the new section *Teretiuscula* within subgen. *Euparmelia* for *P. pubescens* and *P. minuscula* with rounded fruticose to subfruticose lobes and no rhizines. In doing this, he seems to have been unaware of the earlier introduction of the generic name *Pseudephebe* by Choisy (1930) for that group; Choisy speculated,

³ Bibliographic citations of usages of a name later than the one in which the name was originally established.

TABLE 1. *Gyelnik's (1932) system for the parmelioid lichens*

Parmelia Ach. 1803

Subgen. *Hypogymnia* Nyl. 1881

Sect. *Tubulosae* Bitt. 1901

 Subsect. *Bitterianae* Gyeln. 1932

 Subsect. *Neonebulosae* Gyeln. 1932

Sect. *Solidae* Bitt. 1901

Subgen. *Menegazzia* (Massal.) Vain. 1890

Subgen. *Bicornuta* Lyngb 1914

Subgen. *Euparmelia* Nyl. ex Hue 1885–6

 Sect. *Everniiformes* Hue 1899

 Sect. *Melaenoparmeliae* Hue 1899

 Sect. *Vainioëllae* Gyeln. 1932

 Subsect. *Protofuscae* Gyeln. 1932

 Subsect. *Neofusca* Gyeln. 1932

 Sect. *Xanthoparmeliae* Vain. 1890

 Subsect. *Endoleuca* Vain. 1890

 Subsect. *Endocoeeruleae* Gyeln. 1931

 Subsect. *Endoxanthae* Vain. 1890

 Subsect. *Hypotrachynae* Vain. 1890

 Subsect. *Sublineares* Vain. 1890

 Subsect. *Cyclocheileae* Vain. 1890

 Subsect. *Irregulares* Vain. 1890

 Sect. *Olivascentes* Harm. 1909

 Sect. *Subflavescentes* Vain. 1890

 Subsect. *Eciliatae* Gyeln. 1932

 Subsect. *Ciliatae* Gyeln. 1932

 Sect. *Subglaucoscentes* Vain. 1890

 Subsect. *Eciliatae* Gyeln. 1932

 Subsect. *Ornaticolae* Gyeln. 1932

 Sect. *Epicypheclatae* Gyeln. 1932

in a diagrammatic evolutionary tree, that *Pseudophebe* was derived from *Bryopogon* (i.e. *Bryoria*) and leading to the foliose *Melaenoparmelia*, a generic name he presumably based on Hue's sectional name although he did not attribute it to him⁴. Hillmann's work is particularly notable for the large numbers of infraspecific taxa recognized, some of which later proved to have merit. The following year, Degelius (1937) introduced the new generic name *Cavernularia* for inflated *Hypogymnia*-like species with narrow lobes and perforation-like depressions in the lower cortex.

⁴ This generic-level usage is not mentioned in Esslinger (1977) and never appears to have been catalogued, but has to be treated as not validly published under Art. 33.3 (last sentence) as there was no reference to Hue's infrageneric usage and no description was provided or species names mentioned.

The first major work on the group in North America then appeared (Berry (1941), in which 56 species were accepted, dispersed through the subgenera *Menegazzia*, *Hypogymnia*, *Euparmelia* (with four sections), and *Pseudevernia*. Of especial note, in addition to Berry's very detailed descriptions and ecological information, were the reduction of *Pseudevernia* to subgenus, and the recommendation that *Parmelia saxatilis* be selected as the type species of *Parmelia* (*loc. cit.*: 32). Räsänen (1943) went on to reduce *Cavernularia* to a section of *Hypogymnia*, and adopted a neater infrageneric system within *Parmelia*, recognizing eight discrete sections: *Amphigymnia*, *Bicornuta*, *Cyclocheila*, *Hypotrachyna*, *Melanoparmelia*, *Pseudoparmelia*, *Sublinearis* and *Xanthoparmelia*.

Krog (1951) applied chemical reagent and especially microcrystal tests to the parmelioid lichens, recognizing *Hypogymnia* and *Pseudevernia* at generic rank, but like Räsänen she did not accept *Cavernularia* as distinct from *Hypogymnia*; she also used the chemical products to support the exclusion of the *Parmelia alpicola* group from *Hypogymnia*. Asahina (1952), however, was more conservative, maintaining both *Hypogymnia* and *Menegazzia* as subgenera in his treatment of the Japanese species. He did, however, distinguish two subsections within subgenus *Euparmelia* sect. *Hypotrachyna*: subsect. *Myelochroa* for species with a yellow or orange medulla, and subsect. *Myeloleuca* for ones with a colourless medulla. Yet perhaps the most foresighted worker on the classification of parmelioid lichens at this time was Choisy (1952). Choisy resurrected and emended Massalongo's *Parmotrema* to embrace sections *Amphigymnia* and *Hypotrachyna* (including subsections [?] *Irregularis*, *Regularis*⁵ for the *Parmelia borreri* group, and *Sublineares*) and combined *Parmelia saxatilis* and allied species into *Parmotrema*. The circumscription of *Parmelia* was emended to include only sections *Xanthoparmelia*, *Melanoparmelia* and *Cyclocheileae*.

⁵ No description was included and Choisy attributed the name to himself.

Dodge (1959) raised *Amphigymnia* to sub-generic rank, and also reinstated *Omphalodium*, characterized by umbilicate thalli, to its original rank of genus rather than subgenus.

The *Code* produced after the 8th International Botanical Congress in Paris in 1954 was the first to include a list of conserved generic names of lichens (Lanjouw *et al.* 1956). Amongst these was *Parmelia* which was conserved with *P. saxatilis* as the type species, as recommended by Berry (1941), not *P. conspersa* as selected by Clements & Shear (1931; see above). This proposal had been unanimously approved by the Special Committee for Lichens (Ahlner 1954), and as each edition of the *Code* is endorsed by the successive congress this choice has to be regarded as approved⁶.

1960–1973

Poelt (1962) accepted *Hypogymnia* as a genus, and this decision was quickly followed by North American authors in particular. Lamb (1964) transferred Hillman's sect. *Teretiuscula* species back into *Alectoria* where they had been placed by earlier workers.

The overview of *Parmelia* subgenus *Parmelia* by Hale & Kurokawa (1964) marked a revival of interest in the genus. They endorsed the choice of *P. saxatilis* as type species, and *Amphigymnia* and *Xanthoparmelia* were also recognized as subgenera. Within subgen. *Parmelia*, five sections, four subsec-

tions, and two series were recognized; these included the new subsection *Simplices* for *Parmelia borrieri* and related species, and a new series name was coined, sect. *Bicornuta* ser. *Relicinae*. Keys to species were provided, but descriptions were largely restricted to those new to science or for which new names were required. The brown species were omitted from their scheme as they had "yet to decide on their exact position in the genus" (*loc. cit.*: 121). This work was quickly followed by a detailed and exhaustive revision of subgenus *Amphigymnia* by Hale (1965), who selected *P. tinctorum* as its type. He regarded colour as "useless as a sectional character" but agreed with Gyelnik that cilia were important. Two sections were distinguished in the subgenus, *Amphigymnia* (syn. *Subglaucescentes*) for species that lacked marginal or apical cilia, and *Subflavescentes* for ones with ciliate margins and apices; the latter section was divided into two subsections (*Subflavescentes* for species without maculae and *Ornaticolae* for ones with maculae) each of which had two series separated by thallus colour and the positions of rhizines.

Culberson & Culberson (1968) separated out the *Parmelia cetrarioides* group from *P. sect. Amphigymnia* into a new genus *Cetrelia*, emphasizing the marginal pycnidia and consistent absence of marginal cilia. They stressed the generally perforate apothecia, thick subhymenium, larger ascospore size, bifusiform conidia, and chemical products in separating *Cetrelia* from *Platismatia*.

1974–1996

This is the period which witnessed an explosion in the number of new genera being segregated or resurrected from *Parmelia*. The starting shots were fired in 1974, when in a single year Hale re-introduced *Parmotrema* (Hale 1974a), raised *Hypotrachyna* (Hale 1974b), *Relicina* and *Xanthoparmelia* all to generic rank (Hale 1974c), and also described two new genera, *Bulbothrix* (including sect. *Bicornutae*), and *Parmelina* (Hale 1974c). These decisions were based primarily on differences in thallus lobe shapes, colour, marginal cilia, and rhizine types.

⁶ Brusse (1988) points out that this list of names of lichen genera for protection by conservation had originally been drawn up by Zahlbruckner in 1930, and that it was included in the *Code* produced after the Cambridge Congress (Briquet 1935: 127–129). Zahlbruckner did not select any species as type, and who added the types included in Ahlner (1954) is uncertain. Brusse questioned whether the conservation process had been correctly followed as there was no evidence of the list with types being formally presented for approval to the Paris or a later Congress, and so the validity of this typification could be in doubt. Although this might have been desirable as precluding the need for numerous transfers into *Xanthoparmelia* that subsequently became necessary, Brusse's view cannot be upheld because of the formality of ratifying the entire *Code* (i.e. including the Appendices with lists of conserved names) by each immediately following Congress (cf. Greuter *et al.* 2000: 15).

Everniastrum quickly followed for species formerly placed in subgenus *Everniiformes* (Hale 1976d), and *Pseudoparmelia* was extended to include *Parmotrema*-like species with a pored epicortex and rather adpressed narrow lobes with no marginal cilia (Hale 1976c).

Hale did not deal with any of the brown species in the 1974 series of papers as they were the subject of a monograph being prepared by Esslinger (1977). In that work, Esslinger presented extremely detailed accounts of characters used in the systematics of the group and very full descriptions. He accepted 107 species dispersed through two subgenera, *Allantoparmelia* (rhizines absent) and *Melanoparmelia* (rhizines present); the latter subgenus had four sections, *Melanoparmelia* (dark, narrow-lobed, and saxicolous), *Neofusca* (brown or brown-black, usually HNO₃+ blue-green, saxicolous or terricolous), *Olivascentes* (*P. acetabulum* group), and *Vainioëllae* (paler brown, broad-lobed, mainly on bark or wood). Interestingly in view of later developments, Esslinger pointed out the similarities and probable relationships of subgenus *Neofusca* to *Xanthoparmelia*, and of *Melanoparmelia* and *Simplices*. The fruticose to subfruticose genus *Pseudophebe* was naturally not treated by Esslinger as clearly alectoroid in thallus anatomy, but was re-instated by Brodo & Hawksworth (1977). Clearly influenced by Hale's more restrictive generic concepts, Esslinger (1978) went on to recognize three separate genera: *Allantoparmelia*, *Melanelia* (for subgen. *Melanoparmelia*), and *Neofuscelia* (for subgen. *Neofusca*). Presciently, he distinguished three subgenera within *Melanelia*: *Melanelia*, *Olivascentes* and *Vainioëllae*.

Such extensive changes did not gain rapid acceptance outside North America, and even there some dissenting views were expressed (Dey 1978). Beltman (1978) conducted a critical analysis of vegetative and ontogenetic characters in the family, including genera as circumscribed by Hale, which was illustrated by superb scanning electron micrographs; she rejected Hale's system on the basis of the ontogenetic studies in particular.

Krog & Swinscow (1979) raised *Parmelia* sect. *Hypotrachyna* to subgenus and discussed the typification of pertinent supra-specific names; they were convinced that it was a natural group, but considered the characters separating it were "not of great importance at generic level". These sentiments were echoed by Hawksworth *et al.* (1980) who refrained from adopting most of the additional macrolichen genera recognized in the 1970s where there were "no correlations with ascocarp or pycnidial differences". The generic segregates were not adopted by, for example, Poelt & Vězda (1981), Krog & Swinscow (1981) and Clauzade & Roux (1986). At the International Botanical Congress in Sydney in 1981, some problems with the generic circumscriptions were highlighted by the presentation of cell-wall composition data by Imshaug, from the studies of Ralph S. Common; his results on parmelioid lichens were never formally published, although the methodology was much later (Common 1991). At the same Congress, Krog (1982a) drew attention to the occurrence of four main conidium types in the parmelioid lichens which had not received much attention up to that time. Hale's emphasis on macroscopic features in generic circumscriptions had been motivated by pragmatic reasons, a way to sort quickly the huge collections he had been making in the tropics into manageable units (Hafellner *et al.* 1994).

Further genera continued to be separated out through the 1980s. Sipman (1980) introduced *Cetrariastum* for the former section *Everniiformes*, which he separated from *Everniastrum*. Culberson & Culberson (1981), however, did not accept *Everniastrum* and instead accepted 22 species in *Cetrariastum*, and introduced *Concamarella* for two South American species with a chambered upper cortex containing algae. Esslinger (1981) introduced *Albornia* for two saxicolous subfruticose South African species, lacking rhizines, and with a dense chondroid medulla and a cortex unchanged or most faintly green-blue with HNO₃. Krog (1982b) used differences in the type of pseudocyphellae in the recognition of *Punctelia*, with two

subgenera differing in cortical compounds and conidium type: subgen. *Punctelia* with atranorin and unciform to filiform conidia (the *Parmelia borneri* group), and subgen. *Flavopunctelia* with usnic acid and bifusiform conidia (the *P. flaventior* group). Influenced by studies on conidium types in the family, Krog & Swinscow (1983) decided to accept *Parmotrema* after all, and later also adopted *Hypotrachyna*, *Pseudoparmelia* and *Xanthoparmelia* (Krog & Swinscow 1987).

Hale (1984b) then raised *Flavopunctelia* to generic rank, and went on to introduce *Arctoparmelia* for *P. centrifuga* and similar species with usnic acid in the cortex, a velvety lower cortex, a pored epicortex, and cell wall chemistry (Hale 1986). Three new genera were introduced by Elix *et al.* (1986b) for white medulla segregates from *Pseudoparmelia* s. str. with a yellow medulla: *Canoparmelia*, *Paraparmelia*, and *Relicinopsis* distinguished from each other primarily by cortical and medullary compounds, but supported by small differences in ascospore size ranges, ecology and distributions. The saxicolous arctic-alpine *Brodoa* was separated from *Hypogymnia* by virtue of the generally stuffed rather than lax medulla, cortex anatomy and larger ascospores (Goward 1986). *Flavoparmelia* was introduced for species formerly referred to *Pseudoparmelia* but with usnic acid rather than atranorin in the cortex, and bifusiform rather than filiform conidia, differences in medullary chemistry, and thick-walled ascospores (Hale 1986b). In revising *Xanthoparmelia* in Australasia, Elix *et al.* (1986b: 165), while adopting Hale's concept, noted similarities to *Neofuscelia* and some species then placed in *Pseudoparmelia*, and commented: "Whether or not this genus will ultimately accommodate grey and brown, usnic acid deficient, saxicolous species remains to be determined".

Nevertheless, despite such suspicions, the trend of circumscribing more genera continued. Elix & Hale (1987) separated out five genera from *Parmelina*: newly describing *Canomaculina*, *Parmelinella*, *Parmelinopsis*, and *Parmotremopsis*, and raising *Myelochroa* to generic rank. These five genera were dif-

ferentiated on the basis of the medullary compounds, marginal cilia, lobe width, and ascospore sizes. At the International Botanical Congress in Berlin in 1987, Hale distributed a document listing the 26 genera he then accepted in *Parmeliaceae* ("excluding cetrarioid groups, *Pseudevertonia*, and *Hypogymniaceae*" but actually also fruticose genera) with a figure indicating his personal view of their relationships (Fig. 1) which does not appear to have ever been formally published; it is presented here in view of its historical interest.

Awasthi (1987) introduced *Parmelaria* for two Himalayana *Parmotrema*-like species with dark wart-like pycnidia and large ascospores. *Pleurosticta*, originally described as a lichenicolous coelomycete growing on a parmelioid lichen (Petraik 1931), but found to be based on the regular cylindrical to fusiform conidia of *Parmelia acetabulum* (Santesson 1949), was resurrected by Lumbsch *et al.* (1988); they also discovered that it differed from other species that had been placed in *Melanelia* in having a pored epicortex.

Three genera were segregated from *Xanthoparmelia* around this time: *Namakwa* for a single South African saxicolous species with pseudocyphellae and uniseriate ascospores (Hale 1988); *Psiloparmelia* for two species, one Central and South American and the other from southern Africa, distinguished by a velvety lower cortex lacking rhizines, and the absence of lichenin (Hale 1989a); and *Karooovia* for 16 mainly South African saxicolous species with almost crustose thalli with almost placodioid margins, sometimes rhizoid-like attachments or bare below, and rather long cylindrical conidia (Hale 1989a).

Also recognized around this time was *Rimelia* for 12 species of *Parmotrema*-like lichens (the *Parmelia reticulata* group) with distinct, fine white reticulate-maculate upper cortices, sometimes breaking open along the cracks (Hale & Fletcher 1990). *Rimeliella*, also with a reticulate-maculate surface, was introduced by Kurokawa (1991) for seven other species formerly placed in *Parmotrema* but distinguished on the basis of having

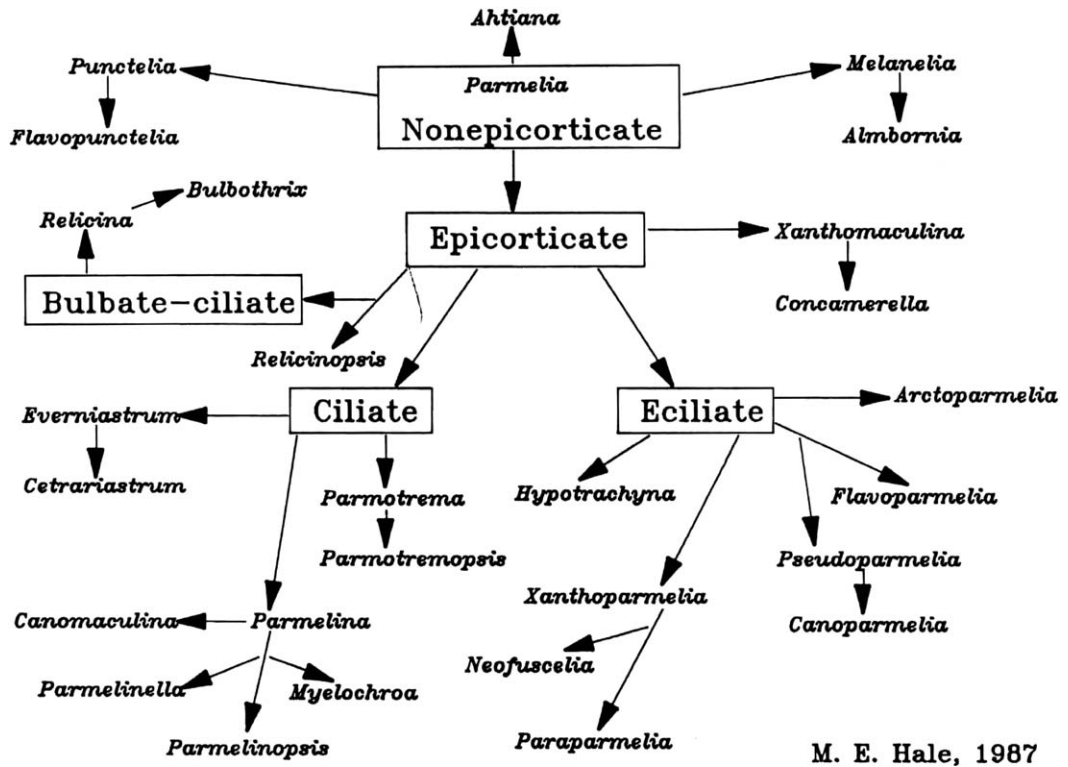


FIG. 1. Hale's schematic representation of the relationship between the parmelioid lichen genera he recognized, presented at the XIVth International Botanical Congress in Berlin in 1987.

mixed short and long rhizines and often sparsely branched marginal cilia; several species also produced usnic acid in the cortex.

More recently, Kurokawa (1994) proposed a new subgenus *Nipponoparmelia* to include a group of East Asian species previously placed in *Parmelia* s. str. (Hale 1987) that differed morphologically from other species in the genus in the lateral, punctate pseudocyphellae. Later, Marcano *et al.* (1996) segregated *Bulbotricella* to include the single species *Bulbothrix amazoniensis*, which occurs in the Venezuelan Amazon and exhibits several singular features, notably multi-spored asci, obovate and acrogenous conidia, and a pored epicortex.

Unease about general acceptance of this increasing number of new generic names continued through the 1980s into the 1990s. A common practice that developed was to

continue to use *Parmelia* in a broad sense, but also cite the segregate names or give them as an alternative (e.g. Santesson 1984; Awasthi 1988; Purvis *et al.* 1992). Poelt (1991) was especially concerned about the use of cortical compounds (i.e. atranorin *vs.* usnic acid) as a generic criterion. Nimis (1993: 471) commented that "at least in some cases, the characters which are utilized for defining the new genera are more appropriate for infrageneric units", but he did accept *Allantoparmelia* and *Parmotrema*. Brusse (e.g. Brusse 1993) continued to use and describe novel species in *Parmelia* in the broad sense. The issue was hotly debated at an international meeting on ascomycete systematics in Paris in 1993, where Hawksworth acknowledged that there certainly were monophyletic groups within *Parmelia* s. lat. that would be recognized as corroborating evidence was obtained (Hafellner *et al.* 1994).

The need for some synthesis was becoming critical, and sadly Hale's tragic death at the age of only 62 in 1990 precluded him from ever doing that; when one of the authors (DLH) last met him at the Smithsonian Institution on 28 June 1989, he was struggling to complete his monograph of *Xanthoparmelia*. In the event, that work treating 406 species was published posthumously (Hale 1990), but in this he reflected on the history of studies of that group, and discussed the taxonomic importance of the characters used in species separation. For more information on Hale's work and the development of his concepts, see DePriest (1999). In an issue of *The Bryologist* dedicated to Hale, Elix (1993) prepared the much-needed and extremely valuable synopsis of the 63 genera then being accepted in *Parmelia* s. lat., including a synoptic key. In this work, Elix recognized that the problem to be addressed was not so much grouping but ranking.

1997–2010

The advent of molecular systematics in the mid-1990s provided an independent method of testing the phylogenetic significance of characters for the first time, as well as the monophyly of any proposed genera. The molecular age now made progress towards an international consensus on generic concepts in the parmelioid feasible.

The first attempt to test phylogenetic relationships and generic circumscriptions in the segregates from *Parmelia* (parmelioid) appeared in 1998 (Crespo & Cubero 1998). This preliminary work was based on a single locus (rDNA nuclear ITS), and only 15 genera were included. Most of the genera Hale had segregated formed monophyletic clades, but others did not. The brown parmelioid *Neofuscelia* clustered within the yellow-green *Xanthoparmelia*, and the reticulate-maculate *Rimelia* within non-reticulated *Parmotrema*. However, the marker used was highly variable for suprageneric treatments, and being a single marker and including only a modest number of lineages, relationships amongst the genera were not well-supported. This pioneering phylogeny, together with two cla-

distic analyses of morphological and chemical features (Crespo *et al.* 1999; Louwhoff & Crisp 2000), suggested that these traits were not suitable for the inference of phylogenetic relationships either. Louwhoff & Crisp (2000) indicated that *Rimelia* and *Canomaculina* might be better treated as subgenera of *Parmotrema*. Further, as a result of studying abundant material from South Africa, Esslinger (2000) noted that the HNO₃+ blue-green reaction previously used in support of the recognition of *Neofuscelia* was absent in "a significant number of southern African species" but present in several members of *Paraparmelia* and *Xanthoparmelia* from the region.

In a further molecular phylogeny of the group, Crespo *et al.* (2001) enlarged the data set, including species belonging to 30 genera in the family (with the type species of 21). In this work the mitochondrial DNA (mtDNA) SSU region was supported as a suitable locus to play a major role in establishing the phylogeny and circumscription of generic concepts in parmelioid lichens. Some clades identified appeared to correlate with differences in cell wall carbohydrates, epicortical extrolites, and other features. Moreover, this molecular marker indicated new relationships among genera and provided better support to inner nodes.

New morphological or chemical studies were also gradually becoming available to clarify and complement the molecular information. One of the most interesting foci was the circumscription of *Xanthoparmelia*, which was first described to include yellow-green species with usnic acid in the cortex. Elix (2003) subsumed *Paraparmelia* within *Xanthoparmelia*. *Paraparmelia* had been distinguished by the absence of usnic acid, but it was synonymized on the basis of morphological and chemical evidence. This decision marked the start of the development of a new circumscription for *Xanthoparmelia*. After that, several studies using multilocus molecular data showed the *Xanthoparmelia* lineage to be by far the largest group of parmelioid lichens. Moreover, chemical and morphological features, a peculiar cell-wall lichenan (xanthoparmelia-type, Elix 1993),

and other synapomorphies such as the smaller ascospores (Elix 1993) with arachidiform vacuoles (Del Prado *et al.* 2007) also supported this monophyletic group. The circumscription of the genus was then enlarged to include *Neofuscelia*, *Chondropsis*, some species of *Karoovia* (Blanco *et al.* 2004a), later *Almbornia*, *Namakwa* and *Xanthomaculina* (Thell *et al.* 2006), and more recently also *Karoovia*, *Omphalodiella* and *Placoparmelia* (Amo de Paz *et al.* 2010 a, b).

In several other groups of genera, the results of molecular phylogenetic studies paralleled those found in *Xanthoparmelia*. Multilocus molecular analyses revealed another large lineage including *Parmotrema*, and several genera which nested within that genus were synonymized, notably *Rimelia*, *Concamerella* and *Canomaculina* (Blanco *et al.* 2005). Interestingly, compared with other parmelioid clades, species of this lineage characteristically have larger ascospores with a thickened outer layer (epispore).

In contrast to the situation in *Xanthoparmelia* and *Parmotrema*, however, molecular studies revealed that *Melanelia* was polyphyletic and two new genera were described (*Melanelixia* and *Melanohalea*; Blanco *et al.* 2004b). Similarly, *Hypotrachyna* (Divakar *et al.* 2006, 2010) also proved to be polyphyletic, and *Remototrachyna* was described as an independent lineage accommodating mostly species from south-east Asia. Further, analyses of *Parmelina* species revealed two groups meriting recognition as genera; *Parmelina* included species from Eurasia, and the new genus *Austroparmelina* ones from Australasia (Crespo *et al.* 2010b).

However, all these studies demonstrate that the parmelioid lichens constitute a monophyletic group, supported by multilocus data sets (Blanco *et al.* 2006; Crespo *et al.* 2007, 2010a) and make it one of the best phylogenetically investigated groups of lichenized fungi. Indeed, 75 % of the species are gathered into a monophyletic cluster where the main relationships are well-known; in this cluster are *Parmotrema*, *Flavoparmelia*, *Austroparmelina*, *Flavopunctelia*, *Punctelia*, *Canoparmelia*, *Xanthoparmelia*, and *Cetrelia*. The remaining 25 % of species

are included in genera where the relationships are not yet as clear. This minority group comprises *Hypotrachyna* and other smaller genera, including *Parmelina* and *Myelochroa*, *Parmelia* s. str., *Melanelixia*, *Melanohalea*, *Nipponoparmelia*, and *Bulbothrix* (Crespo *et al.* 2010a). Tropical and subtropical lineages have evolved faster than those from temperate or cooler regions and the acceleration may be due to the largest number of generations occurring in mild environments (Lumbsch *et al.* 2008).

Our current understanding of the relationships amongst the parmelioid lichens is summarized in Figure 2, and the current application of the generic names of parmelioid lichens is given in Table 2.

Characters used in generic circumscriptions

The extensive molecular data now available in the parmelioid lichens permits an assessment of the phylogenetic value of different characters at the generic level. However, as stated by Lumbsch (1998: 365): “a character by itself has no taxonomic value *a priori* but may have importance when correlated with other independent characters. This however, can only be evaluated *a posteriori*”.

Ascomata

The position of apothecia has traditionally been used to distinguish the cetrarioid and parmelioid groups of genera within *Parmeliaceae*: cetrarioid genera are characterized by marginal apothecia, while parmelioid genera are distinguished by laminal apothecia. Recent molecular studies have shown that the genera *Cetrelia* and *Parmelaria*, previously considered as cetrarioid lichens, belong to the parmelioid group, while *Melanelia* s. str. is actually cetrarioid. That *Parmelaria* is found to be a synonym of *Parmotrema*, suggests that this character is shared for most species of all genera of cetrarioid lichens, but is not universally of value in generic classifications (Blanco *et al.* 2004b, 2005; Thell *et al.* 2009; Crespo *et al.* 2010a). Similarly some



genera, notably *Karoozia* and *Omphalodiella*, are characterized by having the apothecia immersed in the thallus (Hale 1989a; Henssen 1991). However, Amo de Paz *et al.* (2010b) synonymized *Karoozia* and *Omphalodiella* within *Xanthoparmelia*, finding this of no importance at the generic level.

Perforate apothecia are a particular feature of *Parmotrema*, though they do not occur in all species of the genus; we have not encountered them in any other parmelioid genus although they do occur in *Cetrelia* and *Platismatia* (Culberson & Culberson 1968). Ascum anatomy has largely been ignored in taxonomic studies of parmelioid lichens, based on the assumptions that they are uniform within the group, and also because they are rare or unknown in many species. Some preliminary scanning electron micrographs suggested that there could be significant differences in the structure of the true (cupular) exciple in a range of parmelioid lichens (Sincock 1982), but this aspect remains in need of more critical studies only recently initiated (Z. Ferencova, unpublished data). However, it has recently been shown that *Remototrachyna* differs from *Hypotrachyna* in the anatomy of the cupular exciple, in the thickness of the hyphal walls, and this is supported in the molecular phylogeny (Divakar *et al.* 2010). Similarly, Australasian species of *Parmelina* and some *Canoparmelia* species are now being accommodated in the newly described lineage *Austroparmelina*, which differs from *Parmelina* in having a cupulate exciple consisting of a plectenchyma with thick hyphal walls (Crespo *et al.* 2010b).

The only detailed ontogenetic study of parmelioid lichen remains that of Letrouit-Galinou (1970) on *Xanthoparmelia conspersa*. All asci are of the lecanoralean-type, but Thell *et al.* (1995) distinguished eight ascus “forms” with the alectorioid and parmelioid lichens which were different from the cetrari-

oid. It is evident that these characters merit further scrutiny, but this requires critical transmission-electron microscopic (TEM) studies based on freshly collected material of a wider range of species in order to make an objective estimate of its value. Similarly, whether or not there are differences in interascal (hamathecial) elements, for example in their branching and apical structures, has yet to be studied in depth.

Ascospore characters have historically received scant recognition in taxonomic studies of parmelioid lichens, although Ahti (1966) has already noted their importance as specific characters in the brown corticolous species. Their size and shape have been considered of value at the generic level in *Parmeliaceae* (Elix 1993, 1994; Divakar & Upreti 2005), and as more attention is devoted to them it is becoming clear that ascospore features are as important in the family as in other lichenized and non-lichenized ascomycetes. Thick-walled ascospores are a particular feature of the *Parmotrema* clade, and a distinctive vacuolar body appear as a synapomorphy in the *Xanthoparmelia* clade; in all species of the latter genus so far examined, the vacuolar body is arachiform (Del Prado *et al.* 2007).

Conidiomata

In some earlier classifications, the position where the conidiomata arose was regarded as significant. Indeed, the parmelioid group was distinguished from the morphologically similar cetrarioid group in having laminal immersed pycnidia as opposed to marginal emergent pycnidia. However, in the current classification, *Parmelaria* with marginal emergent pycnidia belongs with the parmelioid lichens (Crespo *et al.* 2010a). The anatomical structure of the pycnidial walls, however, has hardly been investigated.

FIG. 2. A simplified consensus modern phylogenetic tree of the parmelioid and similar lichens, based on that of Crespo *et al.* (2010a). The molecular tree was obtained from a Bayesian analysis of a 3-gene dataset. An asterisk (*) on the branches represents supported nodes. The sizes of triangles are in proportion to the number of species described in each genus.

TABLE 2. Current state of generic names in parmelioid lichens. Accepted names are indicated in bold face and synonyms in italics.

<i>Almbornia</i> Essl. 1981 = <i>Xanthoparmelia</i>
<i>Arctoparmelia</i> Hale 1986 ^{*7}
Austroparmelina A. Crespo <i>et al.</i> 2010.
<i>Bulborrhizina</i> Kurok. 1994 [†]
Bulbothrix Hale 1974
<i>Bulbotrichella</i> V. Marcano <i>et al.</i> 1996 = <i>Bulbothrix</i>
<i>Canomaculina</i> Elix & Hale 1987 = <i>Parmotrema</i>
Canoparmelia Elix & Hale 1986 [‡]
<i>Chondropsis</i> Nyl. 1879 nom. rej. = <i>Xanthoparmelia</i>
<i>Concamerella</i> W.L. Culb. & C.F. Culb. 1981 = <i>Parmotrema</i>
Cetrariastrum Sipman 1980 [‡]
Cetrelia W.L. Culb. & C.F. Culb. 1968
Emodomelanelia Divakar & A. Crespo 2010
Everniastrum Hale ex Sipman 1986 ^{††}
Flavoparmelia Hale 1986
Flavopunctelia Hale 1984
Hypotrachyna (Vain.) Hale 1974 [‡]
<i>Karoozia</i> Hale 1989 = <i>Xanthoparmelia</i>
<i>Melanelia</i> Essl. 1978 ^{*8}
Melanelixia O. Blanco <i>et al.</i> 2004
Melanohalea O. Blanco <i>et al.</i> 2004
Myelochroa (Asahina) Elix & Hale 1987
<i>Namakwa</i> Hale 1988 = <i>Xanthoparmelia</i>
<i>Neofuscelia</i> Essl. 1978 = <i>Xanthoparmelia</i>
Nesolechia A. Massal. 1856 ⁹
Nipponoparmelia (Kurok.) K.H. Moon <i>et al.</i> 2010
<i>Omphalodiella</i> Henssen 1991 = <i>Xanthoparmelia</i>
<i>Paraparmelia</i> Elix & J. Johnst. 1986 = <i>Xanthoparmelia</i>
<i>Parmelaria</i> D. D. Awasthi 1987 = <i>Parmotrema</i>
Parmelia Ach. 1803 nom. cons.
Parmelina Hale 1974
Parmelinella Elix & Hale 1987
Parmelinopsis Elix & Hale 1987 [‡]
Parmeliopsis (Nyl.) Nyl. 1866 nom. cons.
Parmotrema A. Massal. 1860
<i>Parmotremopsis</i> Elix & Hale 1987 [†]
<i>Placoparmelia</i> Henssen 1992 = <i>Xanthoparmelia</i>
Pleurosticta Petr. 1931
<i>Pseudoparmelia</i> Lyngé 1914 [†]
Punctelia Krog 1982
Relicina (Hale & Kurok.) Hale 1974
Relicinopsis Elix & Verdon 1986 [‡]
Remototrachyna Divakar & A. Crespo 2010
<i>Rimelia</i> Hale & A. Fletcher 1990 = <i>Parmotrema</i>
<i>Rimeliella</i> Kurok. 1991 = <i>Parmotrema</i>
<i>Xanthomaculina</i> Hale 1985 = <i>Xanthoparmelia</i>
Xanthoparmelia (Vain.) Hale 1974 nom. cons.

* = Belongs to non-parmelioid groups.

† = Uncertain status because of lack of molecular studies including the type species of the genus.

‡ = Generic status and or circumscription require further study.

Conidia were considered to be of particular importance as taxonomic characters in macrolichens by Choisy in the mid-20th century, but have been accorded little attention by most subsequent workers. The arrangement of the conidiogenous cells was regarded as the basis for the separation of *Parmeliopsis* and *Imshaugia* from the rest of the parmelioids. These two genera have the so-called exobasidial arrangement (the *Psora*-type), while in the main parmelioid clade they are endobasidial (*Parmelia*-type) (Vobis & Hawksworth 1981; Meyer 1982, 1985). However, molecular studies have now shown that *Parmeliopsis* belongs amongst the parmelioids and *Imshaugia* to other non-parmelioid groups (Divakar *et al.* 2006; Crespo *et al.* 2007, 2010a). Thus, the arrangement of the conidiogenous cells appears to be of little value for distinguishing these main groups, though it is useful for generic distinctions.

Conidial type has been used as a correlating feature in several generic delimitations in *Parmeliaceae* (Krog 1982b; Hale 1984a; Elix 1993). *Flavopunctelia* is segregated from *Punctelia*, and *Relicina* from *Bulbothrix*, in having bifusiform and unciform conidia respectively (Hale 1974a, 1984b; Krog 1982b). The evaluation of the significance of conidial shape using molecular markers showed that most of the lineages are supported by consistencies in conidium type: for example, *Flavopunctelia* with bifusiform,

⁷ The genus was segregated from *Xanthoparmelia* by Hale (1986) based on morphological features such as the velvety lower surface with sparse simple rhizines and cetraria-type lichenan in the cell wall. Recent molecular study has placed *Arctoparmelia* in the hypogymnioid clade based on molecular phylogenetic tree topology and the presence of a loosely compact medulla as this feature is shared with other hypogymnioid species (Crespo *et al.* 2007).

⁸ Several molecular studies have established the placement of the type species of the genus (*M. stygia*) in the cetrarioid core (Blanco *et al.* 2004, 2006; Crespo *et al.* 2007, 2010) and thus it is now considered a member of the cetrarioid group. Additionally some other species (e. g. *M. disjuncta*, *M. panniformis*, *M. sorediosa*, *M. tominii*) still not removed from *Melanelia* need further study to clarify their systematic position (Crespo *et al.* 2010). Our ongoing studies suggest that these species should be placed in a separate genus.

⁹ See discussion in the text.

Punctelia unciform, *Relicina* bifusiform, *Bulbothrix* cylindrical, and *Parmeliopsis* with falcate, although *Xanthoparmelia* has species with bifusiform and cylindrical types (Crespo et al. 2010a). These correlations show that conidial type merits more attention in generic circumscriptions, but we stress that critical high-power microscopy using appropriate mountants that do not affect size and shape is necessary for their proper study. Conidia also merit more attention at the species level, as made clear by Culberson & Culberson (1980) who used them to support the separation of two species now placed in *Punctelia*.

Cortical chemistry

Cortical and medullary compounds in lichens and their use as taxonomic characters have been assessed, but only prior to the eruption of molecularly-based phylogenetic studies (Hawksworth 1976; Lumbsch 1998). It was generally accepted that, due to their postulated biological, ecological and consequently evolutionary significance, the cortical compounds had an important role in systematic arrangements (Elix 1993); there was general agreement on the correlation of this character with generic level or higher taxonomic ranks. However, Culberson & Culberson (1970) already cautioned that chemical data were likely to be of most value at the infrageneric level.

Atranorin and usnic acids are the compounds responsible for the grey and yellow-green upper surface, respectively, in parmelioid lichens. Likewise, brown to almost black surfaces are due to melanins. The case of the presence of atranorin and usnic acid usually excluding each other was used to propose the separation of usnic acid containing species of *Lecanora* under the resurrected generic name *Straminella* (Pérez-Ortega et al. 2010). Moreover, differences in the anatomy of groups of *Lecanora* species with atranorin and *Lecanora* species with usnic acid supported the dichotomy. However, deeper investigations showed that in many cases species shared crossed characters, concluding that it “does not mean that

all taxa in *Lecanora* with usnic acid will remain in the genus, but it is clear that there is not a simple dichotomy” (Lumbsch 1998).

Some parmelioid genera were segregated primarily on this feature: for example, *Flavopunctelia* from *Punctelia* (Hale 1984b), *Relicina* from *Bulbothrix* (Hale 1974a), *Paraparmelia* from *Xanthoparmelia* (Elix et al. 1986b), *Flavoparmelia* from *Pseudoparmelia* (Hale 1986b), and *Neofuscelia* and *Melanelia* from *Xanthoparmelia* and other brown *Parmelia* s. lat. species (Esslinger 1978). However, in some other genera of the family, differences in cortical chemistry have been accorded less status and variability allowed within the genus, as in *Canoparmelia* (Elix et al. 1986b), *Hypotrachyna* (Hale 1975), *Parmeliopsis* (Hawksworth 1985), and *Parmotrema* (Hale 1974b). On the other hand, improved analytical techniques (HPLC) have shown that in several cases the presence/absence of compounds was not properly diagnosed previously and has a wider variation than had been assumed (Elix 1993, 2003). Taking note of such variations, Elix (2003) synonymized *Paraparmelia* under *Xanthoparmelia*.

As a result of molecular phylogenetic studies, Blanco et al. (2004a) synonymized *Neofuscelia* (brown upper surface due to melanoid substances) with *Xanthoparmelia* (yellow-green upper surface due to usnic acid) and the study also supported the previous synonymy of *Paraparmelia* (grey upper surface containing atranorin) within *Xanthoparmelia*. The only character that had separated these three genera was the colour of the upper surface. In further molecular studies, three more genera having a brown upper surface, *Almbornia*, *Omphalodiella* and *Placoparmelia*, clustered within *Xanthoparmelia* and so were also synonymized within it (Thell et al. 2006; Amo de Paz et al. 2010a).

Molecular phylogenetic studies have shown that cortical chemistry (atranorin, usnic acid and melanin) is a homoplastic state in this group of lichenized fungi (Blanco et al. 2004a, 2006; Thell et al. 2006; Crespo et al. 2007, 2010a; Amo de Paz et al. 2010b). These compounds appear to have been lost and gained several times, indicating that the

taxonomic value of these features had been overestimated in previous classifications.

It should be noted that *Relicina* (with usnic acid), which was segregated from *Bulbothrix* (with atranorin), proved to be distant phylogenetically and independently monophyletic (Divakar *et al.* 2006, 2010; Crespo *et al.* 2007, 2010a); this is not an exception as *Relicina* is also distinguished from *Bulbothrix* in having bifusiform conidia.

We conclude that cortical substances alone cannot be used as a key character for generic separations in parmelioid lichens as it was previously supported in parmelioid (Elix 1993) and also in other groups (Hawksworth 1976; Lumbsch 1998).

Fungal wall polysaccharides

Structural polysaccharides in hyphal walls, such as chitin and β -glucan, are fundamental characters in fungal phyla (Bartnicki-Garcia 1968; Adl *et al.* 2005; Kirk *et al.* 2008). The chemical characterization of these complex polysaccharide molecules requires extraction from substantial amounts of material, purification, and mass-spectrography, but differential staining has been used as diagnostic in some cases. The taxonomic utility of this feature was developed in *Parmeliaceae* by Common (Imshaug 1981; Common 1991), who distinguished four major groups of compounds: isolichenan, *Xanthoparmelia*-type lichenan, *Cetraria*-type lichenan, and intermediate-type lichenan. These polysaccharides have been identified by their staining properties with different iodine reagents (Common 1991), but difficulties with the precision of the technique have been articulated (Elix 1993, 1994; Divakar & Upreti 2005).

In spite of difficulties, these structural polysaccharides prove to be diagnostic for some genera of parmelioid lichens, for example *Xanthoparmelia*-type lichenan in *Xanthoparmelia*, *Cetraria*-type lichenan in *Parmotrema*, and isolichenan in *Flavoparmelia* (Elix 1993, 1994). The taxonomic value of these compounds is vindicated by their occurrence in particular molecularly substantiated lineages. In the current generic

system, *Xanthoparmelia* is characterized by *Xanthoparmelia*-type lichenan, and *Parmotrema* by intermediate type lichenan (Blanco *et al.* 2004a, 2005; Crespo *et al.* 2007, 2010a).

It is therefore clear that structural fungal-wall polysaccharides proved to be synapomorphic, suggesting that these are reliable characters for use in the generic circumscription of parmelioid lichens.

Another group of fungal wall compounds which has proved of particular value at the generic level in ascomycetes is the alkali-extractable and water soluble heteromannans (Leal *et al.* 2010). These complex polysaccharides have repeating units and side chains that require NMR studies for their characterization; 39 such compounds have been recognized, and in ascomycetes in general prove to be phylogenetically informative around the generic level and above. However, to date those in any member of Lecanoromycetes have yet to be fully characterized. Gorin & Iacomini (1985) did include *Parmelia sulcata* in a study suggesting that galactomannans were typical of different lichens, but they did not include other parmelioid species. Subsequent studies on *Parmotrema* and *Rimelia* species revealed such small differences in galactomannans and glucans that it was suggested that these did not support the separation of those two genera (Carbonero *et al.* 2005a, b). However, a small pilot study on a few selected species drawn from a wider range of parmelioid genera that we conducted to assess the efficacy of the approach in this group, gave problematic results (A. Prieto, J. A. Leal, A. Crespo & D. L. Hawksworth, unpublished data) and has yet to be evaluated further.

Surface features

The pioneering scanning electron microscopic study by Hale (1973) revealed a suite of characters that he later emphasized in generic separations. He discovered that some had a thin 0.6–1 μm thick polysaccharide layer above the cortical hyphae, for which the term “epicortex” was proposed by Hawksworth (Hale 1973), while some did not, as in *Pseudevernia* where the surface

comprised the stubby hyphal tips. In species with an epicortex, he found that the layer could either be continuous (non-pored) or be perforated by minute discrete pores (pored) which were generally roughly circular but sometimes tended to coalesce, forming fenestrations observable as faint imprecise bleached spots (Blanco *et al.* 2004). The surfaces could appear quite smooth, or be reticulately maculate. The pseudocyphellae occurred in species with a non-pored epicortex; they were structurally more complex and did not originate in the same way as epicortical pores (Hale 1981).

All these features were used in generic separations, for example *Canomaculina* and *Rimelia* were segregated from *Parmelina* and *Parmotrema* in having effigurate white and reticulate maculae respectively (Elix & Hale 1987; Hale & Fletcher 1990). Louwhoff & Crisp (2000) suggested that *Canomaculina* and *Rimelia* should be included in *Parmotrema* based on a cladistic study of morphological and chemical features, and this was confirmed by subsequent molecular phylogenetic studies, later *Canomaculina* and *Rimelia* being formally synonymized under *Parmotrema* by Blanco *et al.* (2005).

A pseudocyphellate upper surface, with or without a non-pored epicortex, was regarded as a key character for distinguishing *Cetrelia*, *Flavopunctelia*, *Parmelia* s. str., *Pleurosticta*, and *Punctelia* from other parmelioid genera (Krog 1982; Hale 1984*b*, 1987). Most of these genera formed monophyletic groups in molecular phylogenetic studies (Wedin *et al.* 1999; Crespo *et al.* 2001, 2007, 2010*a*; Blanco *et al.* 2005, 2006; Lumbsch *et al.* 2008). However, *Parmelia* s. str. proved to be polyphyletic and a generic rank was subsequently accorded to the species included in *Parmelia* subgen. *Nipponoparmelia*; that independent monophyletic lineage is corroborated by the presence of marginal round pseudocyphellae (Crespo *et al.* 2010*a*). *Melanelia* s. lat., as circumscribed by Esslinger (1978), included brown parmelioid lichens all with a negative reaction to HNO₃, but with or without pseudocyphellae. In the molecular phylogenetic study of Blanco *et al.*

(2004*b*), three independent groups were found within this concept, and two were described as new genera: *Melanelixia* with a pored epicortex and no pseudocyphellae, and *Melanohalea* with a non-pored epicortex and pseudocyphellae.

It must, however, be recognized that all “pseudocyphellae” are not necessarily homologous. Feuerer & Marth (1997) pointed out that in those of *Flavopunctelia* and *Punctelia*, areas of the cortex are missing so that the medullary tissues reach the surface (*Punctelia*-type), whereas in 140 other members of the family investigated these represented altered areas of the cortex where the polysaccharide matrix had been reduced (*Cetraria*-type).

Molecular phylogenetic inferences of character evolution suggest that the non-pored epicortex (mostly occurring in pseudocyphellate species) appears to have been gained more often than lost in the phylogeny of parmelioid lichens, evolving independently in the *Cetrelia*, *Punctelia*, *Flavopunctelia*, *Parmelia*, *Melanohalea*, and *Nipponoparmelia* lineages (Crespo *et al.* 2007, 2010*a*). Consequently, this feature could be regarded as a key character for generic delimitation in the parmelioid lichens.

Growth forms

Traditionally, growth forms (e.g. crustose, fruticose, foliose, umblicate, peltate) were used as a basis for generic delimitation within *Parmeliaceae*, and indeed in lichenized fungi in general. In the parmelioid lichens, the following growth forms have been employed as generic criteria: subcrustose in *Karoowia* (Hale 1989*a*), peltate in *Omphalodiella* (Henssen 1991), foliose in *Parmelia* (Elix 1993), umblicate in *Xanthomaculina* (Hale 1985), and subfruticose in *Almbornia* (Esslinger 1981). Re-evaluation of these phenotypic features, in the light of molecular data, resulted in the synonymy of several genera *viz.*: *Almbornia*, *Chondropsis*, *Karoowia*, *Omphalodiella*, *Placoparmelia*, and *Xanthomaculina* within *Xanthoparmelia* (Blanco *et al.* 2004*a*; Thell *et al.* 2006; Amo de Paz *et al.* 2010*a, b*).

In several molecular studies, growth forms have been found to be homoplasious (Crespo *et al.* 2001, 2007, 2010a; Schmitt *et al.* 2001; Blanco *et al.* 2004a; Divakar *et al.* 2006; Thell *et al.* 2006; Tehler & Irestedt 2007; Amo de Paz *et al.* 2010a, b), and thus it is clear that they cannot be used as a basis for generic separations in *Parmeliaceae*. This result parallels the situation in several other lichenized families (Grube & Hawksworth 2007).

Especially fascinating is the placement of the lichenicolous fungus *Nesolechia oxyspora*, the type and perhaps only species of the genus, in the parmelioid clade. It has no independent thallus. Although at least three laboratories have yielded this result, some researchers sceptical, especially as the ascospore shape and lack of any distinct exciple is so different from other parmelioid lichens. This fungus is reported from the thalli of 19 genera and 64 species of parmelioid lichens, and there are some statistical differences between the ascospore shapes and sizes found on some different parmelioid hosts (Doré *et al.* 2006).

Cilia and rhizines

The types of marginal cilia and rhizines, and the presence/absence of such features, have been widely used to distinguish genera of parmelioid lichens (Hale 1975, 1976a, b; Sipman 1986; Elix 1993, 1994; Divakar & Upreti 2005). *Bulbothrix* and *Relicina* are distinguished from other parmelioid lichens in having bulbate cilia in which oil globules accumulate in the swollen base (Feuerer & Marth 1997). *Parmelina* and *Parmelinella* are characterized by simple marginal cilia in the axils of lobes and simple rhizines on the lower surface; *Canoparmelia* lacks marginal cilia and has simple rhizines; and *Hypotrachyna* has dichotomous rhizines (Hale 1974a, c; Elix & Hale 1987; Elix *et al.* 1986b). However, in some cases a range of these features has been accepted within a single genus: *Bulbothrix* species may have simple to dichotomous rhizines, *Parmotrema* species marginal cilia or not, *Parmelia* s. str. simple to squarrose rhizines, and *Parmelinopsis* simple to sparsely dichotomous rhizines (Hale 1965, 1976a, 1987; Elix & Hale 1987; Divakar *et al.*

2001). Oil globules may be present in the rhizines as well as in bulbate cilia (Feuerer & Marth 1997); indeed, this appears to be the case in most genera of the family apart from *Xanthoparmelia*, according to unpublished studies by R. S. Common (Hale 1990).

Divakar *et al.* (2006) tested the phylogenetic significance of these features and concluded that none corresponded to the major lineages: for example, *Parmelinopsis* grouped with *Hypotrachyna*, and some species of *Bulbothrix* with *Parmelinella*. In a recent molecular phylogenetic study *Canoparmelia* proved to be polyphyletic; some species were transferred to *Austroparmelina* and others to *Parmotrema* (Crespo *et al.* 2010b). Phylogenetic inference studies of the character states indicate that simple cilia and rhizines have been lost and gained several times, but bulbate cilia have been gained more than lost in parmelioid lichens. These results suggest that while cilia and rhizines are not reliable characters for generic circumscriptions, bulbate cilia may distinguish divergent lineages. Nevertheless, Divakar *et al.* (2005) confirmed that rhizines were useful characters at the species level in *Parmelia* s. str., such as the molecular separation of *P. barroanae* from *P. sulcata* which was supported by the occurrence of simple instead of squarrose rhizines.

Extrolites

Extrolites ('secondary metabolites') are compounds excreted and deposited on the surface of the fungal hyphae which have been used extensively in lichen taxonomy since the mid-19th century. Unlike the cortical compounds (see above), variations in medullary chemical constituents have been used mainly at species level and below in lichen taxonomy. However, there are some exceptions where these metabolic products have been employed as markers in generic rank when marked chemical differences involving different groups of compounds were distinctive; for example between *Cetrelia* and *Platismatia* having orcinol and β -orcinol derivatives and aliphatic acids respectively, and between *Myelochroa* (β -orcinol derivatives, secalonic

acids, and triterpenes) and *Parmelina* (orcinol derivatives or aliphatic acids).

Hawksworth (1976) and Lumbsch (1998) critically discussed and summarized the important role and the historical evolution of extrolites in the taxonomy of lichens. Biochemical information can be chemosyn-dromic, involving suites of biosynthetically related compounds, and compounds that can occur at extremely low concentrations; the sensitivity of detection methods thus has to be considered. There has been little critical study of correlations between medullary chemical variation and phylogeny in the parmelioid lichens. In a re-evaluation of the phylogenetic/taxonomic significance of medullary extrolites, Divakar *et al.* (2006) sought support for divergent lineages in hypotrachynoid lichens but their results were inconclusive; species clustered in one group (Group I) contained orcinol depsides, β -orcinol depsides, orcinol depsidones, β -orcinol depsidones, aliphatic acids and benzyl esters and similar compounds, and these groups of compounds were also found in the divergent lineage Group II, along with bis-xanthenes in some cases. Moreover, the newly described lineage *Remototrachyna* contains orcinol depsides, β -orcinol depsidones and aliphatic acids. Similar results were reported in Crespo *et al.* (2010b), where medullary extrolites did not conclusively support the independent lineage named as *Austroparmelina*. Furthermore, a recent study suggests that the value of extrolites at the species level may have been overemphasized within yellow-green *Xanthoparmelia* species (Leavitt *et al.* 2011). However, Blanco *et al.* (2004b) found orcinol depsides and β -orcinol depsidones to support the phylogenetic lineages *Melanelixia* and *Melanohalea* respectively. Further critical investigations are needed to develop any generalization as to the taxonomic significance of medullary extrolites, but the value of these features may have to be considered case-by-case.

Discussion

Molecular characters are now universally accepted in biology as appropriate tools for

phylogenetic reconstruction and the testing of taxonomic hypotheses. The *Parmeliaceae* is now amongst the better-known families of fungi from a molecular phylogenetic perspective. Molecular phylogeny provides hypotheses showing monophyletic lineages of species. In parmelioid, as in other groups of fungi apart from molecular data, there are few, if any, characters that can be considered truly synapomorphic. The most common situation is that each lineage is characterized by a combination of a low number of morphological or anatomical characters, cell-wall chemistry, cortical chemistry features, and less frequently a peculiar composition of medullary extrolites, and ecological and biogeographic traits.

Crespo *et al.* (2007) already identified some evolutionary traits that emerged as related to morphological features. However, most of the analyzed vegetative features were found not to be synapomorphic and to have been gained and/or lost in many groups; among such characters are, for example, growth form, rhizines and cilia, and presumed gas-exchange structures (e.g. pored epicortex, pseudocyphellae, maculae). In contrast, generative characters related to the apothecia (perforation, ascospore and exciple types), or conidiomata (conidium type) proved to be more constant in monophyletic lineages.

As is the case in ascomycete fungi in general, it is the ascomatal and conidiomatal features that are the most critical for the delimitation and characterization of genera in the parmelioid lichens. The emphasis on these characters in deciding ranks to be accorded to clades also ensures that generic concepts in these lichenized fungi are not inconsistent with those in non-lichenized groups, a charge levied at some of the genera that were proposed in the 1970s and 1980s in particular (see above) and which limited their acceptance. The laminar position of the apothecia, something stressed in the separation from cetrarioid groups, is not a synapomorphy in the parmelioid lichens, but it is a common feature exhibited by most species in all genera. The cupulate exciple is apparently the most important ancestral character in the

family, and it is a synapomorphy in the node relating the core of the family with the crustose genus *Protoparmelia*. The anatomy of this exciple can be correlated with each genus, but that does not mean that each genus is characterized by a particular type of exciple. The previously largely overlooked ascospores have proved to provide several features that are valuable at the rank of genus (e.g. the thickness of the perispore, shape of the vacuolar body, size ranges of variability) and are also highly significant at this level, but again most are not synapomorphic. Exceptionally, *Xanthoparmelia* presents a peculiar type of small ascospores and it is of special interest that this genus, showing the highest number of synapomorphies, is the first lineage to have become separated from the rest of the parmelioid clade in the course of evolution, at about 50 Myra (unpublished data from our research group).

In a similar way to the ascospores, the conidia are also found to be an important character in the definition and circumscription of genera, with different conidium types often being consistent within clades. However, this character merits more attention than it has currently received, and needs high-power microscopic observations in appropriate mountants.

The use of cortical chemistry has been postulated as a key character in the recognition of genera, but while the molecular phylogenetic work has substantiated its importance to the characterization of genera, that proves not to be as critical as formerly expected. Indeed, in all lineages studied, the cortical extrolites, such as usnic acid, melanins or atranorin, can be gained and lost. In contrast, it seems likely that there is a good correlation with cell wall polysaccharide chemistry in those cases where it has been studied (i.e. *Parmotrema* and *Xanthoparmelia*) but data are currently missing on these features for most clades.

As more genes and more species have been studied during the last 10–12 years, the phylogenetic trees produced have become particularly robust. Further, characters which were not emphasized in earlier classifications, such as ascospore and conidium

types, prove to be significant. In addition, there is a strong correlation between the occurrence of different species of lichenicolous fungi and the clades now being accepted as genera which is indicative of long-term co-speciation, a topic which will be considered in a separate future publication.

The generic system that is now proposed (Fig. 2) can consequently be commended for general use and, as it is based on so many different gene sequences and so many species, no major surprises are to be anticipated as different gene sequences or even whole genome data become available.

We would like to stress that the resolution of the uncertainties over generic concepts in parmelioid lichens has only been achievable through the co-operation of numerous specialists and collectors, and the foresight of different funding agencies. Systematic lichenology, as is the case with systematic mycology in general, is now at a stage where significant progress in phylogenetic reconstruction and revisions of generic concepts require not only a combination of molecular and critical morphological skills, but also the study of large numbers of species/specimens. With the background of experience of work in this group of lichens, we caution against formal changes in taxonomy being introduced in other groups on the basis of preliminary and incomplete data sets. Name changes should only be made when the information from several independent data sets, based on comprehensive taxon sampling, is overwhelming and is likely to be sufficiently robust not to be called into question by fresh studies of additional species in the group.

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