

***Notoparmelia*, a new genus of *Parmeliaceae* (Ascomycota) based on overlooked reproductive anatomical features, phylogeny and distribution pattern**

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Abstract: The importance of the anatomy and fine morphology of reproductive structures for the systematics of the family *Parmeliaceae* is highlighted by the new genus *Notoparmelia*, described here for Australasian species of *Parmelia*. These species were known to form a monophyletic lineage but correlated characters for its delimitation were lacking. A major characteristic used here for the circumscription of this genus is the overlooked apothecial anatomy. The proper exciple is reduced to one layer formed exclusively by large hyphae without any clear branching pattern and embedded in an abundant polysaccharide matrix. This feature differs from the rest of *Parmeliaceae* which have a stratified three-layered proper exciple composed of a thin hyaline layer, intermediate layer and basal cortex-like structure. The anatomy of proper exciple, together with the thickness of spore walls and other morphological characters such as lobe morphology, pseudocyphellae and rhizine type, allow a precise diagnosis of the new genus. The area of distribution is also useful for characterizing this genus. Sixteen new combinations are proposed.

Key words: Australasia, lichens, proper exciple, spore wall, taxonomic characters

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Introduction

For many years, the delimitation of genera in the lichenized fungi was based on morphological, anatomical and chemical characters, and in the last three decades a number of genera were described in *Parmeliaceae* using these features (e.g. Hale 1974*a, b*, 1976, 1984, 1986*a, b*; Culberson & Culberson 1981; Krog 1982; Elix *et al.* 1986; Elix & Hale 1987; Henssen 1991, 1992; Kurokawa 1991; Elix 1993*a*). However, more recently the delimitation of these genera has been re-evaluated based mainly on molecular phylogenies (e.g. Blanco *et al.* 2004*a, b*, 2005; Divakar *et al.* 2006; Thell *et al.* 2006; Wirtz

et al. 2006; Amo de Paz *et al.* 2010; Crespo *et al.* 2010*b*). Phylogenetic studies showed that some genera, circumscribed on the basis of a few morphological and/or chemical characters, were polyphyletic and that some of the smaller monophyletic groups tended to have distinct distribution patterns (Crespo *et al.* 2010*a, b*; Divakar *et al.* 2010). These studies also revealed examples of previously undetected morphological characters of phylogenetic or taxonomic significance (del Prado *et al.* 2007; Crespo *et al.* 2010*a, b*), or allowed segregation of new genera using both molecular and morphological data (Blanco *et al.* 2004*b*).

Parmelia was described by Acharius (1803) in a very broad sense, encompassing a large number of foliose lichens with lecanorine apothecia, including such diverse genera as *Cetraria*, *Lobaria*, *Parmelia* s. lat., *Physcia*, and *Xanthoria*. By the end of the 19th century, *Parmelia* began to assume its modern circumscription, being described as a foliose

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rhizinate genus with laminal apothecia and simple spores (Fries 1861). The controversial history of *Parmelia* with segregation into new genera, followed by synonymization of some of them, is discussed in Hale (1987) and Crespo *et al.* (2011). Hale (1987) included in *Parmelia* s. str. a small assemblage of 38 species, typified by *P. saxatilis*, and 12 new species were later added (Elix 1993b, 2007; Kurokawa 1994; Elix & Kantvilas 1995; Calvelo & Adler 1999; Feuerer & Thell 2002; Divakar *et al.* 2003, 2005; Molina *et al.* 2004, 2011a, b). In its present delimitation, *Parmelia* is a widespread genus with three centres of diversification (Hale 1987), one in boreal-temperate Europe and North America, a second one in eastern Asia and the third one in Australasia.

Parmelia belongs to the major 'parmelioid' clade within the large and widely distributed family *Parmeliaceae*. Parmelioid lichens can be distinguished by their mainly foliose thalli (rarely subcrustose, subfruticose, peltate and umbilicate), the rhizinate lower surface, laminal cupulate apothecia, *Lecanora*-type asci, and simple ellipsoid hyaline ascospores (Blanco *et al.* 2006; Crespo *et al.* 2007, 2010b). The *Parmelia* species are characterized by adnate, sublinear to subirregular lobes without cilia; an upper surface with effigurate pseudocyphellae, lower surface black, rhizinate (rhizines simple, furcate or squarrosely branched); 8 simple spores per ascus; conidia cylindrical or weakly bifusiform, less than 8.0 µm long; with atranorin and chloratranorin in the cortex (Hale 1987).

In a comprehensive molecular study based on a multi-locus dataset of parmelioid lichens (Crespo *et al.* 2010b), the genus *Parmelia* was shown to split into three separate clades: A, B and D (Fig. 1). The first of these, the *Nipponoparmelia* clade (clade A), contains East Asian species (*Nipponoparmelia laevior* and *N. ricasolioides*) that differ morphologically from other *Parmelia* species by having small punctate pseudocyphellae on the lobe edges. This group of species, previously organized by Kurokawa (1994) in the small subgenus *Nipponoparmelia*, was elevated to generic rank (Crespo *et al.* 2010b). A second group of predominantly Australasian species (*Parmelia subttestacea*, *P. crambidiocarpa*, *P.*

tenuirima, *P. cunninghamii* and *P. signifera*) forms a well-supported clade (clade B) but no distinct morphological characteristics were found. A monophyletic clade C, composed of the genera *Relicina* and *Relicinopsis*, is sister group of the Australasian species of clade B, although with very low statistical support. The third group of *Parmelia* (clade D) contains mostly temperate species (*P. saxatilis*, *P. discordans*, *P. serrana*, *P. sulcata* and *P. squarrosa*), with a centre of distribution in the Northern Hemisphere (Crespo *et al.* 2010b).

In a general survey of the morphology and anatomy of the reproductive structures in *Parmeliaceae*, Ferencova (2012) found greater variability than expected, and promising features that could help in the morphological characterization of the genera. Five types of ascospores, based on their size and form together with the thickness of their spore wall, were established for parmelioid lichens: type I, small ascospores (5.0–10.0 µm long) with a thin spore wall (<600 nm); type II, medium-sized ascospores (10.0–15.0 µm long) with a thin to medium spore wall (<1.0 µm); type III, medium to large ascospores (10.0–20.0 µm long) with a thick spore wall (1.0–2.0 µm); type IV, very large ascospores (>20.0 µm long) with a very thick spore wall (>2 µm); and type V, large to very large ascospores (>15.0 µm long) with a thin to medium spore wall (<1.0 µm). In addition, different types of internal organization of the apothecium were found and described, differing mainly in the anatomy of the proper exciple.

The present study aims to find good diagnostic morphological and anatomical characters to circumscribe the monophyletic lineage of Australasian species (clade B) found in the assemblage of *Parmelia*, with special emphasis on ascomata anatomy and ascospore type.

Materials and Methods

Taxon sampling

In the present study, we investigated 23 fertile specimens from the *Parmelia* and *Nipponoparmelia* clades (Crespo *et al.* 2010b). The sampling included two *Nipponoparmelia* species (*N. laevior* and *N. ricasolioides*) that

TABLE 1. Fertile specimens used in this study, with their location and collection details.

Species	Voucher specimens	Locality	Collector (s)
<i>Nipponoparmelia laevior</i>	MAF-Lich 7278	Japan, Hokkaido	H. Harada
<i>N. ricasolioides</i>	MAF-Lich 15526	China, Yunnan, Jian Chuan Co.	A. Crespo et al.
<i>Notoparmelia</i> <i>crambidiocarpa</i>	MAF-Lich 4965	New Zealand, South Island, West Coast	H. A. Imshaug
<i>N. erumpens</i>	MAF-Lich 7529	Australia, Australian Capital Territory	M. C. Molina & J. A. Elix
<i>N. erumpens</i>	MAF-Lich 7576	Australia, New South Wales	M. C. Molina & J. A. Elix
<i>N. signifera</i>	MAF-Lich 7545	Australia, Australian Capital Territory	M. C. Molina & J. A. Elix
<i>N. subtestacea</i>	MAF-Lich 17026	New Zealand, South Island, Otago	A. Knight
<i>N. tenuirima</i>	MAF-Lich 17027	New Zealand, South Island, Southland	A. Knight
<i>N. tenuirima</i>	MAF-Lich 7663	New Zealand, South Island, West Coast	M. E. Hale
<i>Parmelia adaugescens</i>	MAF-Lich 7277	Japan, Hokkaido	H. Harada
<i>P. adaugescens</i>	MAF-Lich 9870	Japan, Hokkaido	H. Harada
<i>P. cochleata</i>	MAF-Lich 7280	Japan, Hokkaido	H. Harada
<i>P. cochleata</i>	MAF-Lich 9880	Japan, Hokkaido	H. Harada
<i>P. fertilis</i>	MAF-Lich 9871	Japan, Hokkaido	H. Harada
<i>P. omphalodes</i>	MAF-Lich 6798	Spain, Madrid	A. Crespo
<i>P. omphalodes</i>	MAF-Lich 15485	Spain, Zamora	A. Crespo & O. Blanco
<i>P. saxatilis</i>	MAF-Lich 12518	Spain, La Rioja	A. Crespo et al.
<i>P. saxatilis</i>	MAF-Lich 11541	Spain, Cadiz	A. Crespo et al.
<i>P. sulcata</i>	MAF-Lich 13883	Spain, Madrid	A. Crespo
<i>P. sulcata</i>	MAF-Lich 15421	Ireland, Kerry Dunkerron	A. Crespo et al.
<i>Parmelina quercina</i>	MAF-Lich 13949	Spain, La Rioja	A. Crespo et al.
<i>Relicina limbata</i>	MAF-Lich 10504	Australia, New South Wales	J. A. Elix
<i>Relicinopsis intertexta</i>	MAF-Lich 15372	Thailand, Nakhon Nayok	W. Polyviam
<i>R. rahegensis</i>	MAF-Lich 15373	Thailand, Nakhon Nayok	W. Polyviam

form clade A; four (*P. subtestacea*, *P. crambidiocarpa*, *P. tenuirima*, *P. signifera*) of the five species included in the Australasian clade B plus *P. erumpens*; three species (*Relicina limbata*, *Relicinopsis intertexta* and *R. rahegensis*) closely related to species of clade C; and six *Parmelia* species (*Parmelia adaugescens*, *P. cochleata*, *P. fertilis*, *P. omphalodes*, *P. saxatilis* and *P. sulcata*), two of them (*P. saxatilis* and *P. sulcata*) included in clade D of the molecular phylogeny (Crespo et al. 2010b). One *Parmelina* species (*P. quercina*) was included for comparison. Details of the material studied (locality and collection data) are summarized in Table 1. In addition, we considered the descriptions of all species of the *Parmelia* assemblage, in particular the Australasian species, found in the bibliography (Hale 1987; Elix 1993a, 2007; Elix & Kantvilas 1995) to complement our own observations.

Morphological studies

Vertical sections through the central part of three apothecia per specimen were cut with a razor blade under the dissecting microscope (Leica Wild M 8) and mounted in water and lactophenol cotton-blue (Panreac, Barcelona). The structure of the sections and morphology of the ascospores were observed and photographed with a light microscope (Nikon Eclipse 80i; Nikon, Badhoevedrop, Netherlands) using Nomarski differential interference contrast optics. The length and breadth of ascospores, and the thickness of their wall, were measured

in 30–50 ascospores per specimen. Mean values of the ascospore size and ratio between length and breadth (Q) were calculated. Thallus morphology of the specimens was studied using a dissecting microscope for the assessment of lobe shape, width and other vegetative features.

Results

The ascospore morphology, together with apothecium morphology and anatomy of fertile specimens of *Nipponoparmelia* (clade A) and three minor clades (B, C and D) of the *Parmelia* clade (Fig. 1), were investigated. The new diagnostic reproductive features based on ascospore type (defined by spore size and spore wall thickness) and structure of the proper exciple are summarized in Tables 2 and 3. These features, combined with the morphological diagnostic characters currently known (Table 4), allow us to clearly separate the four clades. The species of the four clades can be distinguished by a combination of features such as lobe

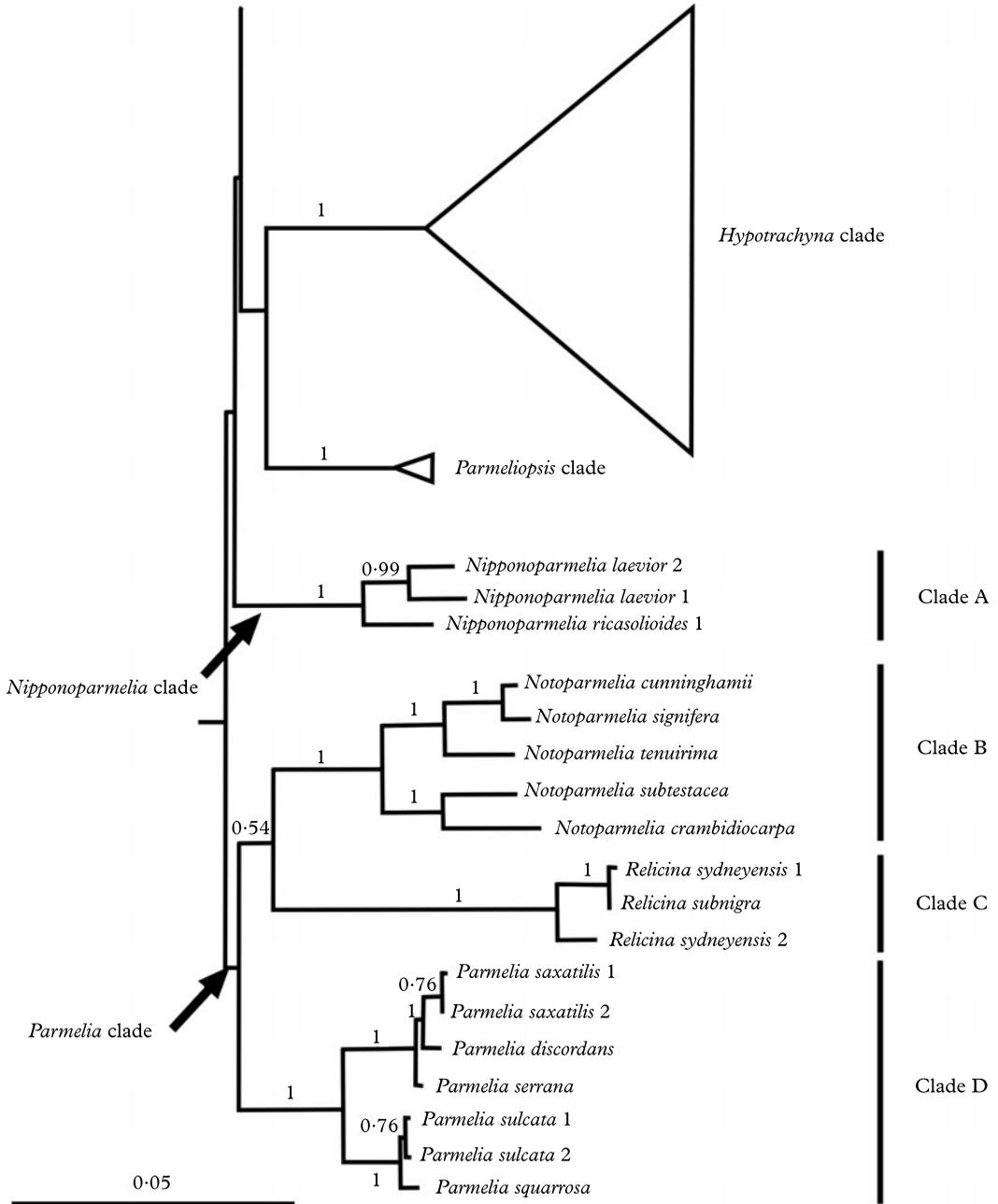


FIG. 1. Simplified tree showing the splitting of the genus *Parmelia* into three independent monophyletic lineages A, B and D (based on Fig. 1 in Crespo *et al.* 2010b; phylogram obtained from a Maximum likelihood analysis of the 3GENE dataset, showing the phylogenetic relationships among *Parmeliaceae*).

TABLE 2. Ascospore dimensions and ascospore type in the species studied, and overall range of dimensions for each genus.

Species	Length mean \pm SD (μm)	Width mean \pm SD (μm)	Wall thickness (nm)	Ascospore type* (Ferencova 2012)	Fig.
<i>Nipponoparmelia laevior</i>	17.75 \pm 0.73	8.41 \pm 0.65	600	V	2A
<i>N. ricasolioides</i>	19.52 \pm 1.03	12.20 \pm 0.97	700	V	2B
<i>Nipponoparmelia</i>	17.0–20.5	7.5–13.0	<1000	Large to very large ascospores with medium walls	
<i>Notoparmelia crambidiocarpa</i>	17.60 \pm 0.48	11.33 \pm 0.53	1000	III	2G
<i>N. erumpens</i>	12.62 \pm 0.54	7.99 \pm 0.44	500	II	2C
<i>N. substestacea</i>	12.43 \pm 0.85	8.42 \pm 0.64	500	II	2E
<i>N. signifera</i>	14.54 \pm 0.90	7.99 \pm 0.51	700	II	2D
<i>N. tenuirima</i>	14.80 \pm 0.68	9.44 \pm 0.77	700	II	2F
<i>Notoparmelia</i>	11.5–15.5(–18.0)	7.5–10.0(–12.0)	\leq1000	Medium (rarely large) ascospores with thin to medium (rarely thick) walls	
<i>Parmelia adaugescens</i>	23.01 \pm 1.52	12.45 \pm 1.09	2800	IV	2K
<i>P. cochleata</i>	12.41 \pm 0.56	6.96 \pm 0.30	1000	III	2J
<i>P. fertilis</i>	14.61 \pm 0.53	7.89 \pm 0.65	1300	III	–
<i>P. omphalodes</i>	13.92 \pm 0.73	8.45 \pm 0.63	1500	III	2L
<i>P. saxatilis</i>	15.08 \pm 0.65	10.95 \pm 0.72	1900	III	2M
<i>P. sulcata</i>	13.39 \pm 0.81	8.55 \pm 0.56	1000	III	–
<i>Parmelia</i>	12.0–16.0(–24.5)	6.5–11.5(–13.5)	\geq1000	Medium to large (rarely very large) ascospores with thick to very thick walls	
<i>Relicina limbata</i>	6.50 \pm 0.54	4.22 \pm 0.34	400	I	2H
<i>Relicinopsis intertexta</i>	6.24 \pm 0.44	4.07 \pm 0.34	400	I	–
<i>Relicinopsis rahegensis</i>	7.16 \pm 0.33	4.18 \pm 0.31	400	I	2I
<i>Relicina</i> + <i>Relicinopsis</i>	6.0–7.5	3.5–4.5	400	Small ascospores with thin walls	

*see Introduction

morphology, rhizine type, pseudocyphella structure, ascospore type (Fig. 2) and structure of the proper exciple (Figs 3 & 4). Chemistry, conidiospore features and ascospore ratio Q overlap and do not help to distinguish these monophyletic groups.

Clade B is described here as a new genus, *Notoparmelia*. The species included in this clade, and all the Australasian species morphologically closely related (formerly included in *Parmelia*) are combined in this new genus.

Ascospores

The ascospore features in the *Nipponoparmelia* and *Parmelia* clades are shown in Table 2 and represented in Fig. 2.

The ascospores of *Nipponoparmelia laevior* and *N. ricasolioides* fit ascospore type V as described for parmelioid lichens (Ferencova 2012). They are large to very large (17.0–20.5 \times 7.5–13.0 μm) with medium spore wall thickness (600–800 nm) (Fig. 2A & B). They are ellipsoidal in *N. ricasolioides* (Q = 1.61) and elongated in *N. laevior* (Q = 2.12).

Notoparmelia erumpens, *N. tenuirima*, *N. signifera* and *N. substestacea* have ascospores of type II, medium-sized (11.5–15.5 \times 7.5–10.0 μm), broadly ellipsoidal to ellipsoidal (Q = 1.48–1.83), and with a thin to medium spore wall (500–700 nm) (Fig. 2C–F). *Notoparmelia crambidiocarpa* ascospores (Fig. 2G) fit type III because they are large (17.0–

TABLE 3. *Main apothecium features in Nipponoparmelia, Notoparmelia, "Relicina + Relicinopsis" and Parmelia s. str. clades.*

Character	<i>Nipponoparmelia</i> (clade A)	<i>Notoparmelia</i> (clade B)	<i>Relicina + Relicinopsis</i> (clade C)	<i>Parmelia</i> s.str. (clade D)
Apothecium	substipitate	stipitate to substipitate, mostly large, splitting radially with age	substipitate	substipitate, rarely large, and splitting radially with age
Proper exciple structure	3-layered: thin to thick hyaline layer thin intermediate layer cortex-like basal layer	1-layered: thick hyaline layer (30–70 µm)	3-layered: thin to thick hyaline layer thin intermediate layer cortex-like basal layer	3-layered: thin to thick hyaline layer thin intermediate layer cortex-like basal layer

18.0 × 11.0–12.0 µm) and ellipsoidal (Q = 1.56), with a thick wall (1000 nm). Another eleven species reported by Hale (1987), Elix (1993a, 2007) and Elix & Kantvilas (1995), which possibly form part of this group because of the morphology and distribution pattern (restricted to Australia and/or New Zealand), were not studied here because of the lack of fertile material, or of any material at all. According to the data provided by those authors, they also have ascospores of type II, medium-sized with a thin to medium spore wall.

Ascospores of *Relicina limbata* (Fig. 2H), *Relicinopsis intertexta* and *R. rahegensis* (Fig. 2I) are of type I, small (6.0–7.5 × 3.5–4.5 µm) with a thin spore wall (400 nm). All the species from both genera have been reported to have small ascospores, corresponding to type I (Hale 1975; Elix *et al.* 1986).

Parmelia cochleata (Fig. 2J), *P. fertilis*, *P. omphalodes* (Fig. 2L), *P. saxatilis* (Fig. 2M) and *P. sulcata* have ascospores of type III; they are medium to large (12.0–16.0 × 6.5–11.5 µm), broadly ellipsoidal to ellipsoidal (Q = 1.38–1.86) with a thick spore wall (1000–1800 nm). *Parmelia adaugescens* (Fig. 2K) has ascospores of type IV, very large (21.0–24.5 × 11.5–13.5 µm), ellipsoidal (Q = 1.80) with a very thick wall (2500–3500 nm). Other species which possibly form part of this group because of the morphological features and distribution pattern

(Hale 1987; Calvelo & Adler 1999; Feuerer & Thell 2002; Divakar *et al.* 2003) were not studied here due to the lack of fertile material. After Hale's description, most of them present ascospores of types III and IV, except two species with ascospores of type I (*P. meiophora* and *P. submutata*).

Anatomy of the apothecium

The most important character found here, and unique for the Australasian clade B, *Notoparmelia*, is the internal structure of the apothecium (Table 3). *Notoparmelia* spp. have large apothecia with the disc usually splitting radially. The proper exciple of those apothecia is formed by a thick cupulate hyaline layer (HL), composed of large hyphae embedded in an abundant polysaccharide matrix (Fig. 3A–E) and surrounded directly by a continuous algal layer. The hyphae of the thick hyaline layer do not show any organization or stratification: they are large and without any clear branching pattern, apparently connecting the subhymenium with the medulla (Fig. 3C–E). In *Notoparmelia tenuirima*, some kind of stratification can be observed and the hyphae in the lower part of the hyaline layer change direction and are vertically orientated (Fig. 3E).

In all other species studied here (clades A, C and D), the fungal hyphae connecting the subhymenium and the medulla (i.e. the hyphae of the proper exciple) form three clearly

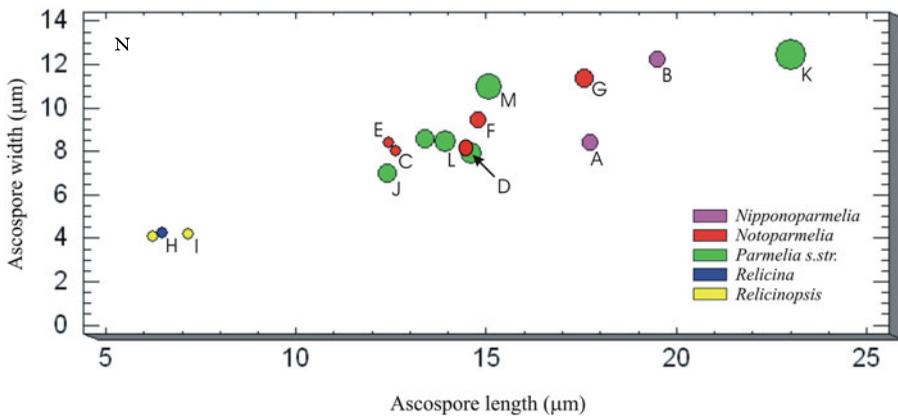
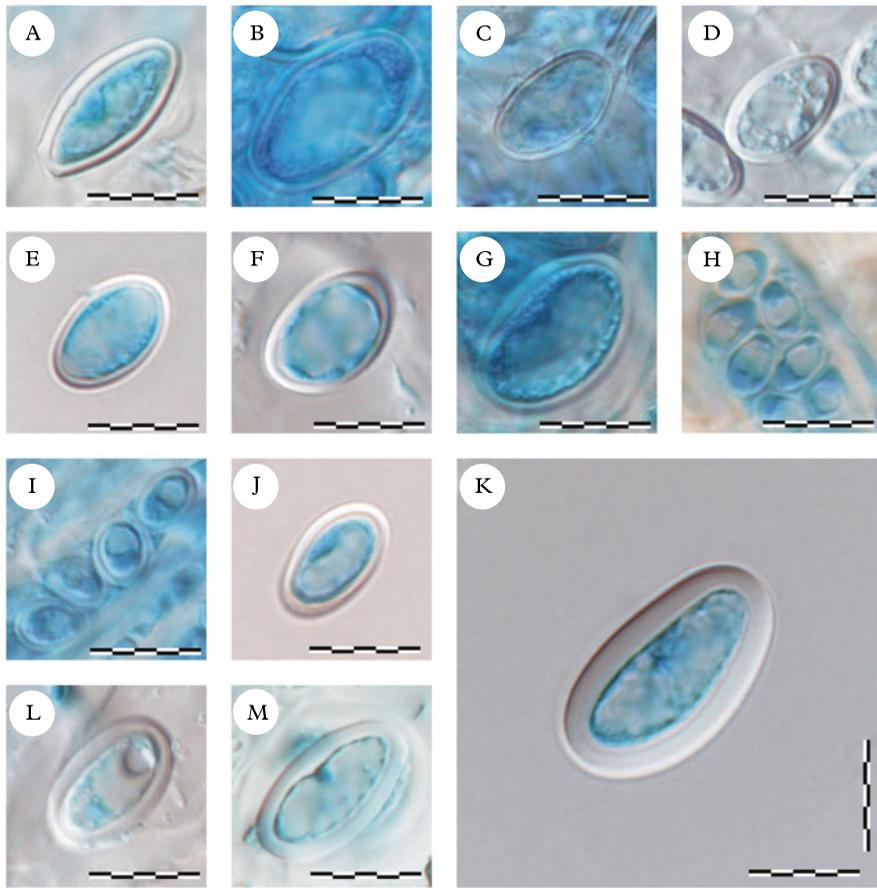


FIG. 2. Ascospore morphology. A, *Nipponoparmelia laevior*; B, *N. ricasolioides*; C, *Notoparmelia erumpens*; D, *N. signifera*; E, *N. subtestacea*; F, *N. tenuirima*; G, *N. crambidiocarpa*; H, *Relicina limbata*; I, *Relicinopsis rahegensis*; J, *Parmelia cochleata*; K, *P. adaugescens*; L, *P. omphalodes*; M, *P. saxatilis*. Bar = 10 μm. The relation between ascospore length and ascospore width in the species belonging to clades *Parmelia* and *Nipponoparmelia* is shown in the box below. The diameter of the circle reflects the relative thickness of the spore wall.

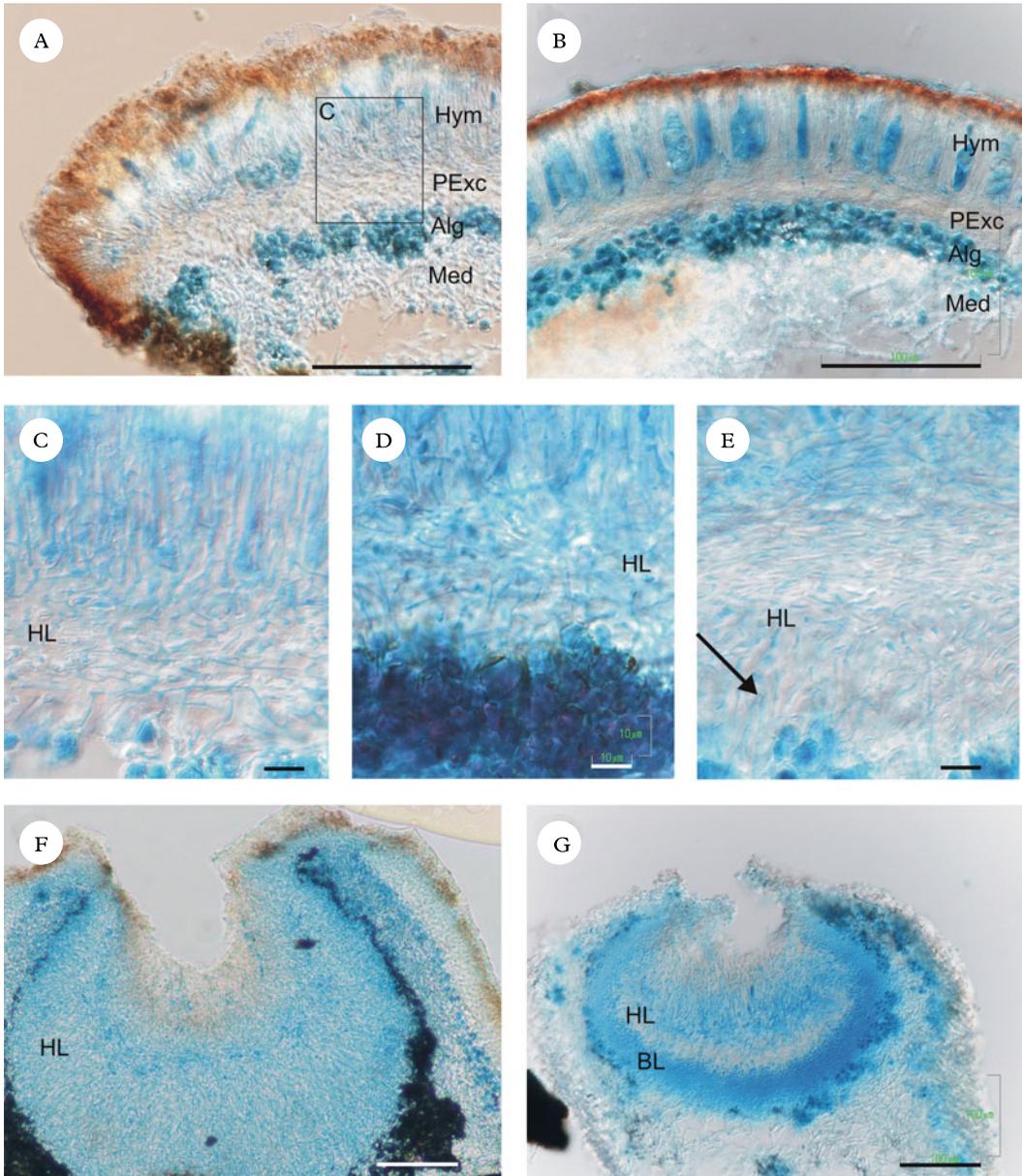


FIG. 3. A & B, cross-section through the apothecium of *Notoparmelia* species; C–E, details showing the cupulate proper exciple F & G, early ontogenic stage of the apothecium. A & C, *Notoparmelia signifera*; B, *N. erumpens*; D, *N. tenuirima*; E, *N. subtestacea*; F, *Notoparmelia tenuirima*; G, *Parmelina quercina*. Alg = algal layer; BL = basal layer; HL = hyaline layer; Hym = hymenium; Med = medulla; PExc = cupulate proper exciple. Scales: A, B, F & G = 100 μ m; C–E: 10 μ m.

differentiated layers (Fig. 4): the thin hyaline layer (HL), the intermediate layer (IL) and the cortex-like basal layer (BL). Differences in the thickness and anatomy of these layers can be observed between different genera (Fig. 4B, D & F) but are not discussed here. In contrast, clade B completely lacks the three-layered organization of the proper exciple present in all other species of clades A, C and D (Fig. 4B, D & F), and in the rest of the *Parmeliaceae* studied (data not shown).

The structure of the proper exciple reflects the organization of the apothecium at the early ontogenetic stages. In the *Notoparmelia* species (clade B), the hyphae between the ascogenous hyphae and the thalline tissue of the young apothecia (Fig. 3F) are radially oriented, and, as mentioned above, the mature apothecium (Fig. 3A, B) has the proper exciple formed by a single layer. In comparison, in all other parmelioid species the developing proper exciple at the same ontogenetic stage is subdivided into an upper hyaline layer and a lower part composed of densely packed hyphae (Fig. 3G). Finally, the mature apothecia of species from clades A (*Nipponoparmelia*, Fig. 4A), C ("*Relicina* & *Relicinopsis*", Fig. 4C) and D (*Parmelia* s. str., Fig. 4E) have a three-layered proper exciple, due to the later differentiation of the lower part into an intermediate layer and a cortex-like basal layer.

Thallus morphology

Both species of *Nipponoparmelia* (clade A) present circular pseudocyphellae along the lobe margins which were not found in any other species studied here. *Relicina* and *Relicinopsis* (clade C) are morphologically very different to all other species included in the present study. They present cilia in the lobe margins and lack any pseudocyphellae. No major differences were found in thallus morphology between *Notoparmelia* (clade B) and *Parmelia* s. str. (clade D). Although some features are typical for clade B (e.g. squarrose rhizines), they can also be found in some species of clade D. No single macromorphological character is suitable for differentiating between these two clades. A summary of the main macromorphological features that characterize the clades is shown in Table 4.

Taxonomy

Notoparmelia A. Crespo, Ferencova & Divakar gen. nov.

MycoBank No.: MB 805031

Thallus foliose, adnate to loosely adnate, irregularly lobate, lobes 2.0–7.0 mm wide; apices rounded. Pseudocyphellae usually effigurate. Rhizines squarrosely branched. Apothecia substipitate to stipitate; splitting radially with age; cupulate proper exciple hyaline and 1-layered, lacking differentiation into three layers as other parmelioids. Ascospores ellipsoid, spore wall less than 1 µm thick. Distribution in Australasia.

Type species: *Notoparmelia signifera*

(Fig. 5)

Thallus foliose, adnate to loosely adnate, irregularly lobate. Lobes flat, narrow, sublinear to subirregular; apices rounded, lacking cilia. *Upper surface* whitish to mineral grey, greenish grey to grey-green, sometimes with brownish tips to the lobes, the pseudocyphellae usually effigurate, sometimes fusing into the continuous white rim around the lobe margins, with or without soredia and isidia. *Medulla* white, loosely packed. *Lower surface* flat, smooth, black or black with brown papillate marginal zone. *Rhizines* short, squarrosely branched. *Ascomata* apothecial, laminal, substipitate to stipitate; *disc* imperforate or rarely perforate, concave, dark to pale brown, splitting radially with age; thalline margin usually pseudocyphellate; cupulate proper exciple consisting of hyaline layer, (30–)40–60(–70) µm thick surrounded by continuous algal layer. *Asci* elongate, clavate, *Lecanora*-type, apically thickened, without an internal apical beak, 8-spored. *Ascospores* medium to large, broadly ellipsoid to ellipsoid, (11.0–)11.5–15.5(–18.0) × (7.0–)7.5–10.0(–12.0) µm; spore wall thin to medium, (400–)600–700(–1000) nm.

Conidiomata pycnidial, immersed, laminal. *Conidia* cylindrical to weakly bifusiform (5.0–)5.5–7.0 × 1 µm long.

Chemistry. Cortex containing atranorin and chloratranorin; medulla containing orcinol depsidones (lobaric acid), β-orcinol depsidones (salazinic, consalazinic, protocetraric and fumarprotocetraric acids), aliphatic acids (protolichesterinic acid), echinocarpic acid and unidentified fatty acid.

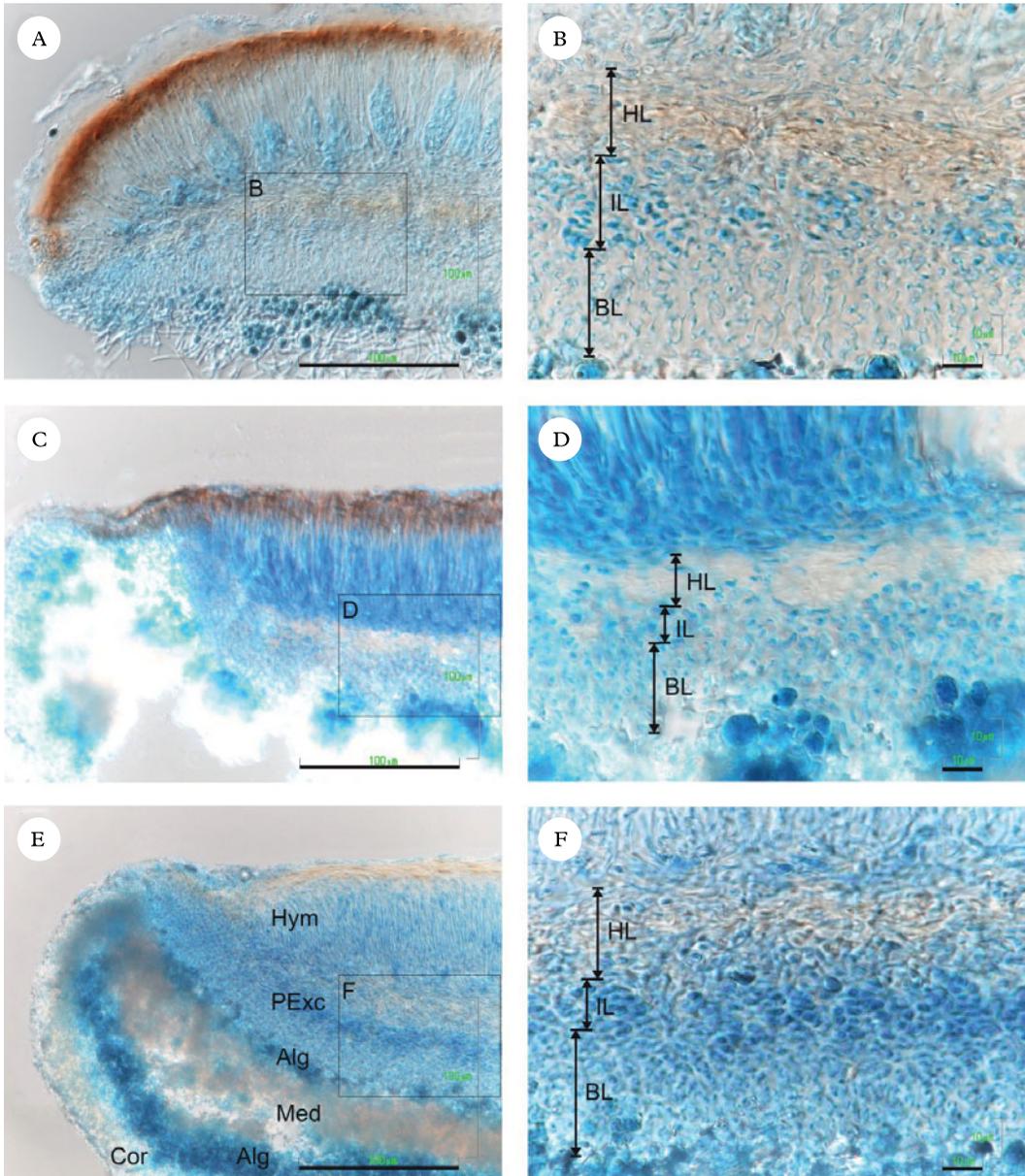


FIG. 4. A, C & E, cross-sections through the apothecia of *Nipponoparmelia*, *Relicina* and *Parmelia* s. str.; B, D & F, details showing three-layered cupulate proper exciple. A & B, *Nipponoparmelia laevior*; C & D, *Relicina limbata*; E & F, *Parmelia adaugescens*. Alg = algal layer, Cor = cortex, Hym = hymenium, Med = medulla, PExc = cupulate proper exciple composed of hyaline layer (HL), intermediate layer (IL) and cortex-like basal layer (BL). Scales: A, C & E = 100 µm; B, D & F = 10 µm.

TABLE 4. Main macromorphological characters and geographical distribution of *Nipponoparmelia*, *Notoparmelia*, “*Relicina* + *Relicinopsis*” and *Parmelia* s. str., based on our observations and bibliographic references (Hale 1975, 1987; Elix 1993a, 2007; Kurokawa 1994; Elix & Kantvilas 1995).

Character	<i>Nipponoparmelia</i> (clade A)	<i>Notoparmelia</i> (clade B)	<i>Relicina</i> + <i>Relicinopsis</i> (clade C)	<i>Parmelia</i> s.str. (clade D)
Lobes	sublinear	sublinear to subirregular	sublinear to linear	sublinear
Pseudocyphellae	small, punctate at lobe edges	effigurate laminal or/and marginal fusing and mostly forming white rim	lacking; pored epicortex present	effigurate laminal or marginal, rarely forming white rim
Rhizines	simple to furcate	squarrosely branched	simple to sparsely branched	simple to furcate and squarrosely branched
Cilia	absent	absent	present	absent
Distribution	East Asia	Australasia (two species also in S America, and one species widespread in S Asia)	Australasia, South-East Asia, Indonesia, India, Neotropical	boreal-temperate Northern Hemisphere



FIG. 5. *Notoparmelia signifera*. A, habit. Scale = 1 cm.

Etymology. The epithet refers to the Southern Hemisphere distribution (*nōto-* in Greek meaning southern, south), and the species superficially resembling *Parmelia*.

Remarks. *Notoparmelia* is characterized by the following combination of characters: sublinear to subirregular lobes with rounded apices, short, squarrose rhizines, substipitate to stipitate large apothecia usually splitting radially with age and having the proper exciple formed only by one layer without stratification (stratified proper exciple in *Parmelia* s. str. with the basal cortex-like structure), and medium to large broadly ellipsoid ascospores ranging from $(11.0-11.5-16.5(-18.0) \times (7.0-7.5-10.0(-12.0) \mu\text{m}$ with thin to medium walls, less than $1 \mu\text{m}$ (more than $1 \mu\text{m}$ in *Parmelia* s. str.). The genus includes 16 species that grow on bark and rocks in southern and eastern Australia, Tasmania and New Zealand. Two species (*N. cunninghamii*

and *N. protosulcata*) also occur in South America, and one species (*N. erumpens*) also occurs in South Africa and is more widespread in East Asia. Species clustered in this genus are mainly distributed in the Southern Hemisphere.

New combinations

We make the following 16 new combinations:

Notoparmelia crambidiocarpa (Zahlbr.) A. Crespo, Ferencova & Divakar comb. nov.

Mycobank No.: MB 805032

Parmelia crambidiocarpa Zahlbr., *Lichenes Novae Zelandiae* 104: 109 (1941).

Notoparmelia crowii (Elix) A. Crespo, Ferencova & Divakar comb. nov.

Mycobank No.: MB 805033

Parmelia crowii Elix, *Mycotaxon* 47: 116 (1993a).

**Notoparmelia cunninghamii (Cromb.)
A. Crespo, Ferencova & Divakar comb.
nov.**

Mycobank No.: MB 805034

Parmelia cunninghamii Cromb., *Journal of the Linnean Society of London* **15**: 228 (1876).

Parmelia brozvnii C. W. Dodge, *Nova Hedwigia* **19**: 449 (1970).

**Notoparmelia erumpens (Kurok.) A.
Crespo, Ferencova & Divakar comb.
nov.**

Mycobank No.: MB 805036

Parmelia tenuirima f. *corallina* Müll. Arg., *Flora* **66**: 46 (1883).

Parmelia erumpens Kurok., *Journal of Japanese Botany* **44**: no.74 (1969).

**Notoparmelia norcrambidiocarpa
(Hale) A. Crespo, Ferencova & Divakar
comb. nov.**

Mycobank No.: MB 805037

Parmelia norcrambidiocarpa Hale, *Smithsonian Contr. Bot.* **66**: 31 (1987).

**Notoparmelia nortestacea (Elix) A.
Crespo, Ferencova & Divakar comb.
nov.**

Mycobank No.: MB 805038

Parmelia nortestacea Elix, *Biblioth. Lichenol.* **95**: 203 (2007).

**Notoparmelia novae-zelandiae (Hale)
A. Crespo, Ferencova & Divakar comb.
nov.**

Mycobank No.: MB 805039

Parmelia novae-zelandiae Hale, *Smithsonian Contr. Bot.* **66**: 31 (1987).

**Notoparmelia queenslandensis (Hale)
A. Crespo, Ferencova & Divakar comb.
nov.**

Mycobank No.: MB 805041

Parmelia queenslandensis Hale, *Smithsonian Contr. Bot.* **66**: 36 (1987).

**Notoparmelia protosulcata (Hale) A.
Crespo, Ferencova & Divakar comb.
nov.**

Mycobank No.: MB 805042

Parmelia protosulcata Hale, *Mycotaxon* **16**: 162 (1982).

**Notoparmelia pseudotenuirima (Gyeln.)
A. Crespo, Ferencova & Divakar comb.
nov.**

Mycobank No.: MB 805043

Parmelia tenuirima f. *isidiosa* Müll. Arg., *Bull. Herb. Bossier* **4**: 90 (1896).

Parmelia pseudotenuirima Gyeln., *Repertorium Specierum Novarum Regni Vegetabilis* **29**: 289 (1931).

**Notoparmelia salcrambidiocarpa (Hale)
A. Crespo, Ferencova & Divakar comb.
nov.**

Mycobank No.: MB 805044

Parmelia salcrambidiocarpa Hale, *Smithsonian Contr. Bot.* **66**: 38 (1987).

**Notoparmelia signifera (Nyl.) A.
Crespo, Ferencova & Divakar comb.
nov.**

Mycobank No.: MB 805046

Parmelia signifera Nyl., *Lichenes Novae Zelandiae*: 25 (1888).

Parmelia saxatilis f. *signifera* (Nyl.) Müll. Arg., *Compte-Rendu Société Royale Belgique* **31**: 30 (1892).

**Notoparmelia substestacea (Hale) A.
Crespo, Ferencova & Divakar comb.
nov.**

Mycobank No.: MB 805048

Parmelia substestacea Hale, *Smithsonian Contr. Bot.* **66**: 45 (1987).

**Notoparmelia tarkinensis (Elix &
Kantvilas) A. Crespo, Ferencova &
Divakar comb. nov.**

Mycobank No.: MB 805050

Parmelia tarkinensis Elix & Kantvilas, *Pap. Proc. R. Soc. Tasm.* **129**: 65 (1995).

**Notoparmelia tenuirima (Hook. f. &
Taylor) A. Crespo, Ferencova & Divakar
comb. nov.**

Mycobank No.: MB 805051

Parmelia tenuirima Hook. f. & Taylor, *Hooker's London Journal of Botany* **3**: 645 (1844).

Parmelia tenuiscypha Taylor, *Hooker's London Journal of Botany* **6**: 175 (1847).

Parmelia tenuirima var. *platyna* Zahlbr., *Lichenes Novae Zelandiae* **104**: 108 (1941).

**Notoparmelia testacea (Stirt.) A.
Crespo, Ferencova & Divakar comb.
nov.**

MycoBank No.: MB 805053

Parmelia testacea Stirt., *Scottish Naturalist* 4: 203 (1878).

Parmelia tenuirima * *P. rudior* Nyl., *Lichenes Novae Zelandiae*: 25 (1888).

Parmelia tenuirima var. *erimis* Nyl., *Lichenes Novae Zelandiae*: 25 (1888).

Parmelia rudior (Nyl.) Zahlbr., *Catalogus lichenum universalis* 6: 198 (1929).

Parmelia erimis (Nyl.) Hillmann, *Hedwigia* 78: 259 (1939).

Parmelia signifera f. *pallidior* Zahlbr., *Lichenes Novae Zelandiae* 104: 107 (1941).

Notoparmelia

This newly described genus includes a group of Australasian species previously placed in *Parmelia* s. str. (Hale 1987) that differ morphologically from other species in this genus by having thinner spore walls and a proper exciple that is reduced to one layer without zonation and composed exclusively of loosely branched large hyphae embedded in an abundant polysaccharide matrix. The proper exciple is surrounded by a continuous algal layer.

Discussion

Notoparmelia, the new genus described here, has been previously shown to form an independent monophyletic lineage of *Parmelia* (Crespo *et al.* 2010b). Although the different distribution pattern of the group was noted (Hale 1987; Crespo *et al.* 2010b), no macromorphological features were known to separate these Australasian species from the rest of *Parmelia*. Here, we offer some overlooked reproductive features that are typical for this lineage, confirming once again the usefulness of the micromorphological and anatomical characters for genus delimitation in *Parmeliaceae* (e.g. del Prado *et al.* 2007; Crespo *et al.* 2010a; Divakar *et al.* 2010).

Relicina and *Relicinopsis* (clade C) form the sister group of *Notoparmelia* (clade B), although with very low support (Crespo *et al.* 2010b). Both groups are sympatric in part of

their area (Australasia) but, independent of their relationship, they are morphologically so different (see Table 4) that they cannot be misidentified. In addition to macromorphological traits (presence/absence of pseudocyphellae and cilia, type of rhizines), the micromorphological differences (anatomy of proper exciple and ascospore type) are also very clear (Figs 2, 3, 4C & D; Tables 2 & 3).

Nipponoparmelia (clade A) contains four species with a special type of circular marginal pseudocyphella, distinct from those of other *Parmelia* species (Crespo *et al.* 2010b). Usually it presents simple to furcate rhizines. Also, the type of ascospores of the species studied differs from the rest of *Parmelia* studied, being of type V (i.e. large ascospores with medium spore wall thickness) (Fig. 2A & B). Moreover, the anatomy of the proper exciple is three-layered in *Nipponoparmelia* (Fig. 4A & B) and so very different to the one-layered proper exciple of *Notoparmelia* (Fig. 3A–E).

On the other hand, *Notoparmelia* (clade B) and *Parmelia* s. str. (clade D) are similar in most of the macromorphological features but in spite of this apparent homogeneity, they differ in fine morphological details, especially the ascospore type (Table 2) and ascoma anatomy (Table 3). The range of their ascospore size overlaps but they differ in the thickness of the spore wall (Table 2, Fig. 2). *Parmelia* s. str. has ascospores of type III and IV, medium to very large, with spore walls more than 1 μm thick (Fig. 2J–M), while *Notoparmelia* has ascospores of type II, medium-sized, with the spore wall of thin to medium thickness, less than 1 μm (Fig. 2C–F), with the exception of *N. crambidiocarpa* (Fig. 2G) which has ascospores of type III (large ascospores with ± 1 μm thick spore wall).

The main distinctive, previously overlooked, character that distinguishes *Notoparmelia* from *Parmelia* s. str. is the internal structure of the apothecia (Figs 3 & 4). Hale (1987) noted that Australasian species of *Parmelia* have large apothecia with the disc splitting radially with age, and a usually broken and inward folded margin. The reason for these features was never investigated and

we offer the hypothesis that these features are probably a consequence of the internal structure of the apothecium. As shown in the results, the proper exciple of *Notoparmelia* is formed exclusively by the thick cupulate hyaline layer, composed of large hyphae without a clear orientation and embedded in an abundant polysaccharide matrix. This is a unique feature that is exceptional in *Parmeliaceae* (although present also in the unrelated genus *Platismatia*, Ferencova 2012). The proper exciple of the *Notoparmelia* apothecium does not show the characteristic stratification of all other *Parmeliaceae*; it lacks the intermediate layer and cortex-like basal layer. The latter is thought to function as a supportive and protective tissue because its composition is similar to the cortical tissue. It is formed by short-branched and interconnected hyphae that probably act as a skeleton which prevents the disruption of the apothecia during changing hydration states. The hydrophilic polysaccharide matrix in which the hyphae are embedded may allow maintenance of the integrity of the whole structure of the apothecia. Why the species of *Notoparmelia* do not present such an organization of the proper exciple is unknown.

Moreover, the geographical areas of the three groups previously included in *Parmelia* are different. *Nipponoparmelia* is distributed in East Asia. *Notoparmelia* is restricted to the Southern Hemisphere, with the centre of distribution in Australia and New Zealand, two species also in South America (*N. cunninghamii* and *N. protosulcata*), and one also widespread in South-East Asia (*N. erumpens*). It should be noted that these three more extended species are sorediate. *Parmelia* s. str. is centred in boreal-temperate Northern Hemisphere areas, although some species are distributed worldwide (Hale 1987; Molina et al. 2004).

The new genus *Notoparmelia* has been shown to form two monophyletic groups (see Crespo et al. 2010b). The first one contains two corticolous species (*N. crambidiocarpa* and *N. subtetacea*), with sublinear to subirregular lobes with an almost continuous white rim around the lobe margins formed by pseudocyphellae. Both species have been

examined in the present study and they show the one-layered proper exciple characteristic for the genus. Two species, *N. norcrambidiocarpa* and *N. salcrambidiocarpa*, were described by Hale (1987) as morphologically identical (whitish grey thalli with the dense rhizines projecting a mat around lobe margins) to *N. crambidiocarpa*. Their differences are related to ascospore size, chemistry and distribution pattern. Due to the lack of fertile material it was not possible to study their apothecial anatomy but, as pointed out by Hale (1987), they have ascospores that fit type II similar to the rest of *Notoparmelia* and, thus, we included both species in the new genus. The case of *N. subtetacea* and *N. nortetacea* is similar. Both species were described by Hale (1987) and Elix (2007), respectively, as morphologically identical (pale greenish to grey thalli with roundish marginal secondary lobes and lower surface black with distinct bare to papillate brown zone around the margins) but differing in chemical pattern from *N. tetacea*. Both were reported to have ascospores that fit into the same ascospore type II (Hale 1987; Elix 2007), and so we also included them in the new genus *Notoparmelia*.

The second monophyletic group of *Notoparmelia* is composed of three species, *N. signifera*, *N. cunninghamii* and *N. tenuirima* (see Crespo et al. 2010b), which morphologically share small effigurate pseudocyphellae. Two of them, *N. signifera* and *N. tenuirima*, show the one-layered proper exciple characteristic for the genus and ascospores of type II. The isidiate counterpart of *N. tenuirima*, *N. pseudotenuirima* (Hale 1987), was not studied due to the lack of material, but is included in the new genus because it was reported to have ascospores of type II (Hale 1987). Similarly, five other species *N. crowii* (Elix 1993a), *N. novae-zelandiae* (Hale 1987), *N. protosulcata* (Hale 1982), *N. queenslandensis* (Hale 1987) and *N. tarkinensis* (Elix & Kantvilas 1995), originally described as *Parmelia* species, are included in *Notoparmelia* because they share morphological traits, distribution area and ascospore type with the rest of *Notoparmelia* species.

More extensive sampling including other species is required to confirm that the molecular based phylogenetic topology parallels the morphological traits, to refine the species concept in this genus and to further confirm the position of all mentioned species within this genus.

Conclusions

The structure of the proper exciple is an important character for *Parmeliaceae* (Crespo *et al.* 2010a; Divakar *et al.* 2010) that has been neglected in systematic studies due to the frequent absence of ascospores in samples. Our results corroborate the segregation of *Nipponoparmelia* based on molecular and morphological vegetative data (Crespo *et al.* 2010b), and indicate that the two monophyletic groups formed by *Parmelia* species clearly differ in anatomical characteristics of the proper exciple, ascospore type and geography. Based on these correlated features, we have proposed the segregation of *Parmelia* into two genera. Since the type species (*P. saxatilis*) is included in clade D, it is considered as *Parmelia* s. str. and clade B (Australasian *Parmelia*) is described as a new genus, *Notoparmelia*.

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