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Towards an integrative taxonomy of *Phyllopsora* (*Ramalinaceae*)

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Abstract: Species identification in the tropical lichen genus *Phyllopsora* is generally challenging and is based on ascospore morphology, vegetative dispersal units, thallus structure and secondary chemistry. As several type specimens are in poor condition and difficult to interpret, it is often unclear how these old names fit with the currently used taxonomy. In the present study, we aim to identify species boundaries in *Phyllopsora* s. str. supported by an integrative approach using multiple sources of evidence. We investigated a substantial amount of herbarium as well as freshly collected material and generated mtSSU and ITS sequence data from most of the described species, including several types. Species delimitation analyses are applied on the gene trees using mPTP and we construct a species tree of both markers with *BEAST, facilitating discussion of species delimitation and sister-relationships. Comparing morphology, chemistry and molecular data, we found that the mPTP analyses split established species repeatedly. Based on our integrative results, we exclude nine species from the genus, resurrect one (*P. melanoglauca* Zahlbr.), reduce two into synonymy with other *Phyllopsora* species and describe five as new to science: *Phyllopsora amazonica* Kistenich & Timdal (which shares the secondary chemistry (atranorin and terpenoid pattern) with *P. halei* chemotype 1, but differs, e.g., in having smaller areolae that are attached to a thinner, white prothallus, and in having more persistently marginate and less convex apothecia), *Phyllopsora concinna* Kistenich & Timdal (which shares the secondary chemistry (atranorin and parvifoliellin) with *P. parvifoliella* and *P. rappiana*, but differs from both in forming larger isidia, having a white prothallus, apothecial margin paler than the disc, and longer and broader ascospores), *Phyllopsora furfurella* Kistenich & Timdal (which is here segregated from *P. furfuracea* based on having a white prothallus and in containing skyrin in the hypothecium (K+ red)), *Phyllopsora isidosa* Kistenich & Timdal (which differs from *P. byssiseda* in forming a more crustose thallus with more delicate isidia, and from *P. isidiotyla* in forming somewhat coarser, less branched isidia) and *Phyllopsora neotinica* Kistenich & Timdal (a neotropical species here segregated from the now exclusively paleotropical *P. chodatinica*, differing in containing an unknown xanthone (not chodatin)). Lectotypes are designated for *Biatora pyrrhomelaena* Tuck., *Lecidea leucophyllina* Nyl., *L. pertexta* Nyl., and *P. brachyspora* Müll. Arg. In total, we accept 54 species in the genus *Phyllopsora*.

Key words: ITS, lichens, molecular phylogeny, mPTP, mtSSU, species delimitation, tropical rainforest

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Introduction

Phyllopsora Müll. Arg. is a genus of crustose to squamulose lichens primarily inhabiting tree trunks and large branches in tropical and subtropical humid woodlands and rainforests. Members of this genus are mostly found on the bark of woody angiosperms but also on rock or bryophytes, rarely on leaves or dead wood (Brako 1991). They occur on a wide range of tree species and do not show any particular host preference (Sequiera & Kumar 2008). Specimens of *Phyllopsora* have been collected at up to 3500 m above sea level but the genus seems to be most diverse in mountain forests at elevations of

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FIG. 1. *Phyllopsora breviuscula*, the type species of *Phyllopsora*, illustrating the typical growth form with squamules growing on a thick prothallus (O L-207949). Scale = 2 mm. In colour online.

500–2500 m (Brako 1991). It is also found in lowland rainforests (Lakatos *et al.* 2006) and even gallery forests in drier areas, but never exposed to direct sunlight (Brako 1991). The genus is generally characterized by a growth form consisting of patches of small squamules or areoles developing on a basal white to reddish brown to dark brown prothallus (Fig. 1; Brako 1991; Elix 2009). Isidia, lacinules, phyllidia or soredia may be common in some species (Timdal 2008). Apothecia are biatorine with simple or 1-septate, hyaline, ellipsoid to fusiform ascospores (5–45 × 0·8–5·0 µm; Elix 2009; Kistenich *et al.* 2018*a*). However, morphological characters may vary considerably within a single species (Swinscow & Krog 1981; Brako 1991), making it difficult to tell the species of *Phyllopsora* apart.

Throughout its taxonomic history, *Phyllopsora* has been placed in various families: initially placed in the *Phyllopsoraceae* Zahlbr. (Zahlbruckner 1907), it was moved to the *Lecideaceae* Chevall. (Poelt 1973), then to the *Cladoniaceae* Zenker (Schneider 1980), back to the *Phyllopsoraceae* (Hafellner 1984), into the *Bacidiaceae* Walt. Watson (Eriksson & Hawksworth 1986), and finally to the *Ramalinaceae* C. Agardh (Lumbsch & Huhndorf 2007). Recently, a DNA-based phylogeny by Kistenich *et al.* (2018*a*) corroborated its affiliation with the family *Ramalinaceae*.

When Müller described the genus in 1894 from New Zealand, he included four species and one variety (Müller 1894). Zahlbruckner (1907, 1921–1940) included additional species based on morphology. Clements & Shear (1931) designated *P. breviuscula* (Nyl.) Müll. Arg. (Fig. 1) as the lectotype of the genus. Later, several species were transferred to *Phyllopsora* or newly described, for example by Lamb (1963), Riedl (1973), Coppins & James (1979) and Schneider (1980). The last publication, however, provided provisional new species combinations only, pending a monographic treatment of the genus ("Eine formale Umkombination der hier neu zu *Phyllopsora* gestellten Taxa muß – wegen der ungeklärten Synonymie – dem Monographen vorbehalten bleiben"; Schneider 1980: 171). Hence, we treat Schneider's combinations as invalid, since he considered them provisional (ICN Art. 36.1). Most of the species later transferred to *Phyllopsora* were originally described in

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Lecidea Ach. Despite a constant increase in the number of *Phyllopsora* species described, a comprehensive monographic treatment of the genus has not been attempted for a long time, probably because species boundaries in *Phyllopsora* are difficult to establish by means of morphological and anatomical characters alone.

The advent of thin-layer chromatography (TLC) for the investigation of lichen secondary metabolites (i.e. lichen substances; Culberson & Kristinsson 1970; Culberson 1972; Menlove 1974) provided new data for understanding the genus and disentangling its species. Swinscow & Krog (1981) provided the first general treatment of *Phyllopsora*, focusing on East African species. They investigated 90% of the types of all previously described species as well as newly collected material using a combination of morphology, anatomy and chemistry to delimit the genus and its species. However, formulating a clear and unambiguous generic delimitation of *Phyllopsora* proved difficult because of the highly diverse morphological characters. The authors regarded the inclusion of a species in *Phyllopsora* as being a question of probability: 'The larger the number of the[se] characters that are combined in a species the more likely is it to be in *Phyllopsora*' (Swinscow & Krog 1981: 220) and made short morphological comparisons to similar genera, such as *Bacidia* De Not. Based on their investigations, Swinscow & Krog (1981) revised the species circumscriptions within the genus, accepting 11 species for East Africa, and provided guidelines for delimiting *Phyllopsora* species in general. At the same time, they emphasized the wide range of intraspecific variation observed in several *Phyllopsora* species and acknowledged that some accepted species may merely represent extreme forms or morphs of highly variable taxa.

The first monographic treatment with a focus on neotropical species was provided by Brako (1989, 1991). Brako reassessed the species circumscriptions in *Phyllopsora* by investigating type specimens of nearly all published names (93 at the time), and by studying her own extensive collections (Brako 1991). She compiled an updated genus description and accepted 18 species, including 11 varieties, based on detailed morphological, anatomical, ecological and chemical investigations. Furthermore, she delimited the genus from other similar genera, namely *Bacidia*, *Bacidiopsora* Kalb, *Biatora* Fr., *Eschatogonia* Trevis., *Physcidia* Tuck. and the newly described genus *Squamacidia* Brako.

Regional treatments of the genus followed: Timdal & Krog (2001) studied freshly collected material from East Africa and the Mascarene Islands, accepting 20 species for that region. The Australian species were subsequently treated by Elix (2006*a*, *b*, *c*, 2009), who described five new species, commented on the taxonomy of *Phyllopsora* and provided valuable chemical information for several other species and related genera. Timdal (2008) studied material from Peru and accepted 20 species, eight of which were described as new. He also reduced the genera *Squamacidia* and *Triclinum* Fée into synonymy with *Phyllopsora*. By including both sorediate and long-spored species, he expanded the genus circumscription. In a study of the genus in the West Indies (Timdal 2011), 34 species were accepted, including four that were new to science. In addition, Mishra *et al.* (2011) described two new species from India, while Kondratyuk *et al.* (2016) described a new species from South Korea. Thus, the number of accepted species in *Phyllopsora* increased from 18 (Brako 1991) to over 70 extant species in only 25 years.

While chemical information proved useful for detecting species boundaries in *Phyllopsora*, it also raised new questions. Whether or not chemotypes are informative for delimiting species of *Phyllopsora* has remained uncertain. Chemotypes may indeed characterize distinct species, but they might also merely represent regional variation. Furthermore, several *Phyllopsora* specimens lack lichen substances, which is highly problematic in the case of sterile species. Thus, challenges remain in species delimitation and reliable identification despite the availability of chemical data. In our experience, *c.* 30% of all phyllopsoroid specimens that lack apothecia, vegetative dispersal units and lichen substances cannot be identified. In these cases, it is also difficult to discover

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potentially undescribed *Phyllopsora* species. With the rise in routine DNA sequence analysis, DNA sequence data now make it possible to test species hypotheses and investigate relationships using molecular phylogenies.

By the end of 2018, more than 130 *Phyllopsora* species names (including synonyms) existed in the literature. Lücking *et al.* (2017*a*, *b*) accept 95 *Phyllopsora* species, while Kistenich *et al.* (2018*a*) later excluded seven species and included two more. In addition to the extant species, two fossil species enclosed in Dominican amber have been described (Rikkinen & Poinar 2008; Kaasalainen *et al.* 2018), both estimated to be *c.* 15–20 million years old. Vegetative thalli reminiscent of those in *Phyllopsora* are also known in other, even unrelated, genera for example *Cladonia* P. Browne. This raises some doubt as to whether these fossils truly belong to the genus *Phyllopsora*. If indeed they do, these findings would give valuable insight into the evolutionary history of *Phyllopsora*, indicating that the genus had existed in its characteristic squamulose form for several million years.

Among the old named species found in the literature, several are known only from the type collection, for example *P. bibula* (Taylor) Swinscow & Krog and *P. subcrustacea* (Malme) Brako. Old type specimens are often small or in poor condition, prohibiting destructive sampling for morphological, chemical or molecular investigation. Clarifying the taxonomic status of such type names remains a challenge, particularly with respect to currently accepted species. In addition, DNA extraction and amplification has proved difficult from tropical lichen material after only a few years or even months of storage (Staiger *et al.* 2006; Weerakoon *et al.* 2012; Gueidan *et al.* 2015).

In a recent molecular phylogeny of the family *Ramalinaceae*, Kistenich *et al.* (2018*a*) included 16 *Phyllopsora* species and showed that the genus, as commonly understood, was polyphyletic. Three species seemingly belonged in the family *Malmideaceae* Kalb *et al.*, two species belonged in *Sporacestra* A. Massal., one in *Bacidia*, one was transferred to *Bacidina* Vězda, and three were placed in the new genus *Parallopsora* Kistenich *et al.* Notably, it was mainly the long-spored and/or sorediate species that were excluded from *Phyllopsora*. The clade containing the type species *P. breviuscula* (i.e. the genus *Phyllopsora*) was resolved as the sister genus of *Biatora*. On the other hand, two *Crocynia* (Ach.) A. Massal. species (i.e. *C. gossypina* (Sw.) A. Massal. and *C. pyxinoides* Nyl.) as well as *Lecidea thaleriza* Stirt. were included in *Phyllopsora* based on their position in the molecular phylogeny. It appears that the typical growth form of *Phyllopsora*, being characterized by areoles or squamules overgrowing a well-developed prothallus (Fig. 1), originated through convergent evolution caused by ecophysiological advantages (Lakatos *et al.* 2006) rather than representing a unique synapomorphy facilitating genus delimitation (Kistenich *et al.* 2018*a*). The overall results of the *Ramalinaceae* study show that additional revisionary work is urgently required for species classified in *Phyllopsora* (Kistenich *et al.* 2018*a*).

In this study, we use an integrative approach to test species hypotheses in *Phyllopsora*. We focus on the currently accepted species while excluding all fossil species as well as old types that cannot be linked to the current taxonomy (i.e. using 64 accepted species as a starting point; see Supplementary Material Table S1, available online). The study is based on morphological and chemical information as well as DNA sequence data from both herbarium specimens and freshly collected material. Our aim was to test correspondence between the traditional species boundaries and species delimitations supported by molecular phylogenies. We treat *c.* 85% of the currently accepted *Phyllopsora* species and discuss the degree of phylogenetic information provided from chemotypes. Based on the results of this integrative taxonomic study, we present an updated species taxonomy of the genus *Phyllopsora*.

Materials and Methods

Taxon sampling

We aimed to investigate specimens of all accepted non-fossil *Phyllopsora* species (see Supplementary

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Material Table S1, available online). One of the authors (ET) has been working on the genus *Phyllopsora* for more than 25 years. The present study is based on our own experience with identifying species. More than 2500 phyllopsoroid specimens, including all available type material (either seen the physical voucher or a digitized image), have been investigated within the last 25 years. We studied *Phyllopsora* material borrowed from the following herbaria: B, BG, BM, CANB, E, GZU, H, HUTPL, MPEG, PDA and TNS. We also received material from the private herbaria of P. Diederich, A. Frisch, D. Killmann, Z. Palice, S. Pérez-Ortega and P. van den Boom. In addition, we used our own collections in ISE, O, UPS and VEN. Fresh material was collected in Brazil, Venezuela and Sri Lanka. Author names for the species studied are provided in Table 1.

Morphology and chemistry

Microscopic sections were cut on a freezing microtome and mounted in water, 10% KOH (K), lactophenol cotton blue, and a modified Lugol's solution in which water was replaced by 50% lactic acid. Amyloid reactions were observed in the modified Lugol's solution after pretreatment in K. The types of upper cortex referred to in this paper (types 1 and 2) are those described by Swinscow & Krog (1981). Crystals of lichen substances were observed using polarized light. Thin-layer chromatography was performed in accordance with the methods of Culberson (1972), modified by Menlove (1974) and Culberson & Johnson (1982). Examinations were made in the three standard solvent systems A, B′ and C; of these, solvent system B′ was preferred for initial analyses. The presence of fatty acids was generally not investigated. Two-dimensional chromatography (Culberson & Johnson 1976) was performed in a small number of cases. Results from morphological and chemical investigations were used to assign specimens to morphospecies.

Molecular laboratory work

Methods for DNA extraction, PCR amplification and DNA sequencing of the mitochondrial ribosomal small subunit (mtSSU) and the entire nuclear ribosomal internal transcribed spacer region (ITS: ITS1, 5.8S, ITS2), as well as the procedures for sequence assembly, followed Kistenich *et al.* (2018*b*). When PCR amplification or Sanger sequencing failed, we used a five-fold dilution of the DNA-extracts as template. We used a local BLAST search for all newly generated *Phyllopsora* sequences against our *Ramalinaceae* dataset (Kistenich *et al.* 2018*a*). We identified the phylogenetic clade (*sensu* Kistenich *et al.* 2018*a*) for each sequence, and subsequently removed all sequences belonging to the *Malmideaceae* (clade A), the *Bacidia*-group (clade C) and the *Parallopsora*-group (in clade D). Only those sequences falling into the *Phyllopsora* s. str. group (in clade F) were used for the present study (Table 1).

Phylogenetic analyses

The mtSSU and ITS sequences were aligned separately using MAFFT v.7.408 (Katoh & Standley 2013) with the E-INS-i algorithm and the nucleotide scoring matrix set to 1PAM / κ=2. We trimmed the ends of the ITS alignment to comprise only the ITS region and deleted the residual 18S and 28S sequence information. Four *Biatora* species (*B. beckhausii*, *B. rufidula*, *B. vacciniicola* and *B. veteranorum*) were included in the alignments and used for rooting in the subsequent phylogenetic analyses. For each dataset, IQ-TREE v.1.6.7 (Nguyen *et al.* 2015) was used for finding the best-fitting nucleotide substitution model among those implemented in MrBayes (i.e. 1-, 2- and 6-rate models), for finding the best partitioning scheme (Chernomor *et al.* 2016; Kalyaanamoorthy *et al.* 2017) and for constructing a maximum likelihood phylogeny with assessment of bootstrap branch support (BS) using 1000 standard non-parametric bootstrap replicates. The mtSSU data were not divided into subsets, whereas we proposed three subsets for the ITS data corresponding to the ITS1, 5.8S and ITS2 regions. We tested this partitioning scheme using the TESTMERGE function. We checked for incongruences between the gene trees generated by IQ-TREE using compat.py (Kauff & Lutzoni 2002) with a 50% branch support cut-off. In addition, Bayesian phylogenetic inference was carried out separately on each dataset with MrBayes v.3.2.6 (Ronquist & Huelsenbeck 2003; Altekar *et al.* 2004) as described in Kistenich *et al.* (2018*a*). The temperature increment parameter was set to 0·01 and 0·04 for mtSSU and ITS, respectively. We projected the posterior probabilities (PP) from the MrBayes analysis onto each IQ-TREE consensus tree with BS values, and collapsed branches with BS < 50 and PP < 0·7. The resulting trees were edited in TreeGraph2 (Stöver & Müller 2010).

Relationships among *Phyllopsora* were investigated by inferring a species tree from the ITS and mtSSU gene trees using StarBEAST (*BEAST) v.2.0.3 (Heled & Drummond 2010) as implemented in the BEAST 2 package v.2.5.1 (Bouckaert *et al.* 2014). *BEAST estimates a species tree from the sequence data under the multi-species coalescent model and handles uncertainty associated with gene trees (Heled & Drummond 2010). Terminals were classified into 63 species approximately following our own revised taxonomy, except that the chemotypes of *P. buettneri* and *P. porphyromelaena* were treated as separate species. We used the best-fitting nucleotide substitution model as suggested by IQ-TREE for each gene with a fixed overall substitution rate. For the clock model, we chose a relaxed lognormal clock (Drummond *et al.* 2006) for each partition. We assumed a linear species tree population size model with a constant root and estimated the population mean. Several operators were adjusted according to suggested output values after conducting a test run. Three Markov chain Monte Carlo (MCMC) runs were conducted with 400×10^6 generations each, sampling every 5000th generation. We assessed convergence of the three runs and the adequacy of sampling using Tracer v.1.7.1 (Rambaut *et al.* 2018). The first 50% of the sampled trees from

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TABLE 1. *Specimens used in this study with the revised taxonomy, voucher information and GenBank Accession numbers provided. New sequences are indicated in bold; accessions can be recognized by the extract number in Figs 2-4; * indicates types; N/A = not applicable; – indicates missing data; ch = chemotype.*

Species	Revised name	Extract	mtSSU	ITS	Country	Year	Voucher
Biatora beckhausii (Körb.) Tuck.	N/A		MG925858	AF282071	Norway	1995	*H. Holien* 6744 (TRH)
B. rufidula (Graewe) S. Ekman & Printzen	N/A		KF662430	KF650981	Germany	1999	*C. Printzen* 5055 (FR)
B. vacciniicola (Tønsberg) Printzen	N/A		MG925861	MG925960	Norway	2013	*J. Klepsland* JK13-L330 (O)
B. veteranorum Coppins & Sérus.	N/A		KF662425	KF650975	Czech Republic	2011	*Malicek & Z. Palice* 14753 (FR)
Crocynia molliuscula (Nyl.) Nyl.	N/A	7359	**MK352275**	–	La Réunion	1996	*H. Krog & E. Timdal* RE18/03 (O)
C. molliuscula	N/A	7360	**MK352276**	–	Mauritius	1991	*H. Krog & E. Timdal* MAU58/02 (O)
Phyllopsora africana Timdal & Krog ch1 *	N/A	509	**MK352138**	**MK352317**	La Réunion	1996	*H. Krog & E. Timdal* RE08/13 (O)
P. africana ch1	N/A	1436	**MK352175**	**MK352348**	La Réunion	1996	*H. Krog & E. Timdal* RE22/09 (O)
P. africana ch1	N/A	4037	**MK352199**	**MK352370**	Thailand	2012	*P. van den Boom* 46982 (hb. v. d. Boom)
P. africana ch2	N/A	477	**MK352122**	**MK352301**	Japan	1995	*G. Thor* 13199 (UPS)
P. africana ch3	N/A	6348	**MK352231**	**MK352401**	Philippines	1994	*P. Diederich* 13345 (hb. Diederich)
P. breviuscula (Nyl.) Müll. Arg.	N/A	528	MG925892	MG925990	La Réunion	1996	*H. Krog & E. Timdal* RE36/18 (O)
P. breviuscula	N/A	1305	MG925893	MG925991	Brazil	1980	*K. Kalb & M. Marcelli* in Kalb, *Lich. Neotropici* 515 (GZU)
P. breviuscula	N/A	2100	**–**	**MK352355**	Philippines	1992	*B. C. Tan* 92-187 (B)
P. breviuscula	N/A	6752	**MK352245**	**MK352412**	New Caledonia	2016	*J. Rikkinen* 35509 (H)
P. breviuscula	N/A	7212	MK352256	MK352422	Sri Lanka	2017	*S. Kistenich & G. Weerakoon* SK1-642 (PDA)
P. buettneri (Müll. Arg.) Zahlbr. ch1	N/A	428	MK352103	MK352283	Thailand	1994	*P. Wolseley & S. Kanajriavanit* s. n. (BM:734816)
P. buettneri ch1	N/A	995	MK352146	MK352322	Thailand	1993	*P. W. James & P. A. Wolseley* 2466a (BM)
P. buettneri ch1	N/A	1041	**MK352160**	**MK352335**	Kenya	2007	*P. Divakar, H. T. Lumbsch & A. Mangold* 19553D (hb. Pérez-Ortega)
P. buettneri ch2	N/A	6464	**MK352239**	**MK352406**	Brazil	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* AM-37 (O)
P. buettneri ch2	N/A	7177	**MK352252**	–	Venezuela	1984	*L. Brako* 8110 (GZU)
P. buettneri ch3	*P. melanoglauca* Zahlbr.	1038	**MK352158**	**MK352333**	Cuba	2006	*S. Pérez-Ortega* s. n. (hb. Pérez-Ortega)
P. buettneri ch3	*P. melanoglauca*	4042	**MK352203**	**MK352374**	Guatemala	2004	*P. van den Boom* 33408 (hb. v. d. Boom)
P. buettneri ch3	*P. melanoglauca*	4740	**MK352213**	**MK352384**	Venezuela	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-232 (VEN)

(*Continued*)

TABLE 1 (*continued*).

Species	Revised name	Extract	mtSSU	ITS	Country	Year	Voucher
P. buettneri ch3	*P. melanoglauca*	4743	**MK352216**	**MK352387**	Venezuela	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-247 (VEN)
P. buettneri ch3	*P. melanoglauca*	6450	**MK352235**	**MK352403**	Brazil	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-408 (O)
P. buettneri ch4	*P. buettneri* ch3	429	MK352104	MK352284	Thailand	1993	*B. Aguirre, P. W. James & P. Wolseley* 2736 (BM)
P. buettneri ch4	*P. buettneri* ch3	493	MK352131	MK352311	Thailand	1994	*P. Wolseley & S. Kanajriavanit* s. n. (BM:1104011)
P. buettneri ch4	*P. buettneri* ch3	6462	**MK352238**	–	Japan	1995	*G. Thor* 13183 (UPS)
P. byssiseda (Nyl.) Zahlbr.	N/A	4737	**MK352211**	**MK352382**	Venezuela	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-220 (VEN)
P. byssiseda	N/A	4739	**MK352212**	**MK352383**	Venezuela	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-229 (VEN)
P. byssiseda 2	*P. isidiosa* Kistenich & Timdal ⋆	1027	**MK352153**	**MK352328**	USA	2006	*J. C. Lendemer* 7765 dupl. (BG)
P. byssiseda 2	*P. isidiosa*	1030	**MK352155**	**MK352330**	Nepal	2007	*L. R. Sharma, L. Olley, A. Cross, M. Joshi & B. Regmi* M16 (E)
P. byssiseda 2	*P. isidiosa*	4035	**MK352197**	**MK352368**	Dominican Republic	2008	*P. van den Boom* 39012 (hb. v. d. Boom)
P. byssiseda 2	*P. isidiosa*	4781	MG925907	MG926004	Brazil	2007	*R. Lücking & E. Rivas Plata* 23302 (SP)
P. byssiseda 2	*P. isidiosa*	6349	**MK352232**	–	Philippines	1994	*P. Diederich* 13210 (hb. Diederich)
P. byssiseda 2	*P. isidiosa*	7251	**MK352267**	**MK352433**	Australia	2006	*J. A. Elix* 38478 (CANB)
P. canoumbrina (Vain.) Brako	N/A	3627	**MK352195**	**MK352366**	Brazil	2014	*R. S. Barbosa, R. Haugan & E. Timdal* 166 (O)
P. chlorophaea (Müll. Arg.) Zahlbr. ch1	N/A	1309	**MK352172**	–	Venezuela	1986	*L. Brako & P. E. Berry* 8685 (GZU)
P. chlorophaea ch2	N/A	529	**MK352145**	**MK352321**	La Réunion	1996	*H. Krog & E. Timdal* RE36/17 (O)
P. chlorophaea ch2	N/A	1051	**MK352165**	**MK352340**	Kenya	2002	*D. Killmann & E. Fischer* s. n. (hb. Killmann)
P. chlorophaea ch2	N/A	SE382	MG925894	MG925992	La Réunion	1996	*H. Krog & E. Timdal* RE08/10 (O)
P. chodatinica Elix ⋆	N/A	513	**MK352139**	–	Australia	1986	*J. A. Elix & H. Streimann* 21023 (O)
P. chodatinica	N/A	1539	**MK352177**	**MK352350**	New Caledonia	2005	*A. Elvebakk* 05:691 (O)
P. chodatinica	N/A	6456	**MK352237**	**MK352405**	Malaysia	2014	*A. Paukov* 2232 (B)
P. chodatinica 2	*P. neotinica* Kistenich & Timdal	505	**MK352137**	**MK352316**	Trinidad and Tobago	2008	*S. Rui & E. Timdal* 10774 (O)
P. chodatinica 2	*P. neotinica*	1023	**MK352149**	**MK352324**	Cuba	2007	*T. Tønsberg* 37923 (BG)
P. chodatinica 2	*P. neotinica*	1438	**MK352176**	**MK352349**	Trinidad and Tobago	2008	*S. Rui & E. Timdal* 10763 (O)
P. chodatinica 2	*P. neotinica* ⋆	4742	**MK352215**	**MK352386**	Venezuela	2015	*M. S. Dahl, J. E. Hernández M., S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-246 (O)
P. chodatinica 2	*P. neotinica*	4769	**MK352222**	**MK352393**	Brazil	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-402 (O)
P. cinchonarum (Fée) Timdal	N/A	439	**MK352105**	–	Thailand	2002	*H. Sipman* 48664 (B)

(*Continued*)

TABLE 1 (*continued*).

Species	Revised name	Extract	mtSSU	ITS	Country	Year	Voucher
P. cinchonarum	N/A	440	**MK352106**	**MK352285**	Japan	2006	*G. Thor* 21521 (UPS)
P. cinchonarum	N/A	4168	**MK352210**	**MK352381**	Venezuela	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-201 (VEN)
P. cinchonarum	N/A	6063	**MK352227**	–	Guatemala	2004	*P. van den Boom* 33395 (hb. v. d. Boom)
P. confusa Swinscow & Krog *	N/A	514	**MK352140**	**MK352318**	Kenya	1972	*H. Krog & T. D. V. Swinscow* K48/177 (O)
P. confusa	N/A	1024	**MK352150**	**MK352325**	Cuba	2007	*T. Tønsberg* 37813 (BG)
P. confusa	N/A	1300	**MK352169**	**MK352343**	Venezuela	1969	*B. Oberwinkler, F. Oberwinkler & J. Poelt* s. n. (GZU)
P. confusa	N/A	3571	**MK352190**	**MK352362**	Ecuador	2014	*M. Prieto* s. n. (HUTPL)
P. confusa	N/A	4741	**MK352214**	**MK352385**	Venezuela	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-237 (VEN)
P. confusa	N/A	7185	**MK352253**	**MK352419**	Cameroon	1999	*A. Frisch & Idi Tamnjong* 99/Ka1213 (hb. Frisch)
P. confusa	N/A	7236	MK352260	MK352426	Sri Lanka	2017	*S. Kistenich & G. Weerakoon* SK1-609 (PDA)
P. corallina (Eschw.) Müll. Arg.	N/A	1316	**MK352173**	**MK352346**	Venezuela	1986	*L. Brako & P. E. Berry* 8659 (GZU)
P. corallina	N/A	4164	**MK352209**	**MK352380**	Venezuela	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-185 (VEN)
P. corallina	N/A	4762	**MK352220**	**MK352391**	Brazil	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-377 (O)
P. corallina	N/A	4775	**MK352223**	**MK352394**	Brazil	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-430 (O)
P. cuyabensis (Malme) Zahlbr.	N/A	449	**MK352107**	**MK352286**	Peru	2006	*E. Timdal* 10258 (O)
P. cuyabensis	N/A	450	MK352108	MK352287	Thailand	1993	*B. Aguirre, P. W. James & P. Wolseley* 2467a (BM)
P. cuyabensis	N/A	1290	**MK352166**	**MK352341**	Venezuela	1996	*J. Hafellner* 53910 (GZU)
P. cuyabensis	N/A	1291	**MK352167**	**MK352342**	Guatemala	1979	*K. Kalb & G. Plöbst* s. n. (GZU)
P. cuyabensis	N/A	2048	**MK352180**	**MK352352**	Bolivia	2008	*A. Flakus & P. Rodriguez* 12792 (O)
P. dolichospora Timdal & Krog *	N/A	515	**MK352141**	**MK352319**	Mauritius	1991	*H. Krog & E. Timdal* MAU65/22 (O)
P. dolichospora	N/A	6357	**MK352233**	–	Papua New Guinea	1992	*P. Diederich* 10847 (hb. Diederich)
P. dolichospora	N/A	6763	MK352247	MK352414	Sri Lanka	2017	*G. Weerakoon* Hg40 (PDA)
P. dolichospora	N/A	6767	MK352248	MK352415	Sri Lanka	2017	*G. Weerakoon* Si113B (PDA)
P. dolichospora	N/A	7258	MK352271	MK352435	Sri Lanka	2017	*S. Kistenich & G. Weerakoon* SK1-643 (PDA)
P. fendleri (Tuck. & Mont.) Müll. Arg.	N/A	2098	**MK352183**	**MK352354**	Costa Rica	1985	*H. Sipman & A. Chaverri* 20806 (B)
P. fendleri	N/A	7473	**MK352277**	**MK352437**	Venezuela	1979	*H. Sipman* 10688 (B)
P. foliata (Stirt.) Zahlbr.	N/A	1035	**MK352157**	**MK352332**	Japan	2004	*H. Kashawadani* 46389 (TNS)

(*Continued*)

TABLE 1 (*continued*).

Species	Revised name	Extract	mtSSU	ITS	Country	Year	Voucher
P. foliata	N/A	7238	MK352261	MK352427	Sri Lanka	2017	*S. Kistenich & G. Weerakoon* SK1-627 (PDA)
P. foliata	N/A	7247	**MK352265**	**MK352431**	Australia	2006	*J. A. Elix* 38235 (CANB)
P. foliatella Elix	*P. foliatella* ch1	7253	**MK352268**	–	Australia	2005	*J. A. Elix* 37286 (CANB)
P. foliatella	*P. foliatella* ch1	7254	**MK352269**	–	Australia	1998	*H. Streimann* 61609 (CANB)
P. furfuracea (Pers.) Zahlbr.	N/A	452	**MK352109**	**MK352288**	La Réunion	1996	*H. Krog & E. Timdal* RE36/22 (O)
P. furfuracea	N/A	453	**MK352110**	**MK352289**	Trinidad and Tobago	2008	*S. Rui & E. Timdal* 10799 (O)
P. furfuracea	N/A	455	**MK352111**	**MK352290**	Peru	2006	*E. Timdal* 10183 (O)
P. furfuracea 2	*P. furfurella* Kistenich & Timdal *	3570	**MK352189**	**MK352361**	Ecuador	2014	*M. Prieto* s. n. (HUTPL)
P. furfuracea 2	*P. furfurella*	4036	**MK352198**	**MK352369**	Dominican Republic	2008	*P. van den Boom* 39069 (hb. v. d. Boom)
P. glaucella (Vain.) Timdal	N/A	1000	**MK352147**	**MK352323**	Dominican Republic	1987	*R. C. Harris* 20779 (BM)
P. glaucella	N/A	2125	**MK352184**	**MK352356**	Argentina	2013	*L. I. Ferraro, A. Aptroot & M. E. S. Cáceres* 10761 (O)
P. glaucella	N/A	4766	**MK352221**	**MK352392**	Brazil	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-393 (O)
P. glaucella	N/A	4780	**MK352225**	**MK352396**	Brazil	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* AM-44 (O)
P. gossypina (Sw.) Kistenich *et al.* ch1	N/A	3575	**MK352192**	**MK352363**	Brazil	2014	*R. S. Barbosa, R. Haugan & E. Timdal* 141 (O)
P. gossypina ch1	N/A	3576	**MK352193**	**MK352364**	Brazil	2014	*R. S. Barbosa, R. Haugan & E. Timdal* 34 (O)
P. gossypina ch1	N/A	4160	MG925867	MG925967	Brazil	2015	*S. Kistenich & E. Timdal* SK1-108 (O)
P. gossypina ch1	N/A	4746	MG925868	MG925968	Brazil	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-287 (O)
P. gossypina ch1	N/A	7201	MK352254	MK352420	Sri Lanka	2017	*S. Kistenich & G. Weerakoon* SK1-584 (PDA)
P. gossypina ch2	N/A	4750	**MK352219**	**MK352390**	Brazil	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-297 (O)
P. halei (Tuck.) Zahlbr. ch2	N/A	457	**MK352113**	**MK352292**	Tanzania	2008	*E. Timdal* 10931 (O)
P. halei ch2	N/A	1044	**MK352161**	**MK352336**	Kenya	2007	*P. Divakar, H. T. Lumbsch & A. Mangold* 19574K (hb. Pérez-Ortega)
P. halei ch3	N/A	7221	MK352257	MK352423	Sri Lanka	2017	*G. Weerakoon* 1008 (PDA)
P. hispaniolae Timdal	N/A	1545	**MK352178**	–	Ecuador	1999	*Z. Palice* 3875 (hb. Palice)
P. hispaniolae	N/A	3569	**MK352188**	**MK352360**	Ecuador	2014	*M. Prieto* s. n. (HUTPL)
P. hispaniolae	N/A	4039	**MK352201**	**MK352372**	Panama	2010	*P. van den Boom* 44158 (hb. v. d. Boom)
P. homosekikaica Elix *	*P. foliatella* ch2	7243	**MK352262**	**MK352428**	Australia	1986	*J. A. Elix & H. Streimann* 20241 (CANB)

(*Continued*)

TABLE 1 (*continued*).

Species	Revised name	Extract	mtSSU	ITS	Country	Year	Voucher
P. homosekikaica	*P. foliatella* ch2	7246	**MK352264**	**MK352430**	Australia	1986	*J. A. Elix & H. Streimann* 20203 (CANB)
P. imshaugii Timdal	N/A	3558	**MK352185**	**MK352357**	Ecuador	2014	*M. Prieto* s. n. (HUTPL)
P. imshaugii	N/A	4043	**MK352204**	**MK352375**	Guatemala	2004	*P. van den Boom* 33433 (hb. v. d. Boom)
P. imshaugii	N/A	4744	**MK352217**	**MK352388**	Venezuela	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-253 (VEN)
P. intermediella (Nyl.) Zahlbr.	*P. longiuscula* (Nyl.) Zahlbr.	454	MG925899	MG925996	Peru	2006	*E. Timdal* 10433 (O)
P. isidiotyla (Vain.) Riddle	N/A	1315	MG925906	MG926003	Brazil	1979	*K. Kalb & G. Plöbst* in Kalb, *Lich. Neotrop*. 343 (GZU)
P. kalbii Brako	N/A	456	MK352112	MK352291	Thailand	1993	*B. Aguirre, P. W. James & P. Wolseley* 2695 (BM)
P. kalbii	N/A	458	**MK352114**	**MK352293**	Tanzania	2008	*E. Timdal* 10913 (O)
P. kalbii	N/A	459	**MK352115**	**MK352294**	Venezuela	1989	*K. Kalb* s. n. (O)
P. kalbii	N/A	1028	**MK352154**	**MK352329**	USA	2010	*J. C. Lendemer* 25770 (BG)
P. kalbii	N/A	2052	**MK352182**	–	Bolivia	2010	*A. Flakus & J. Quisbert* 19221 (O)
P. kiiensis (Vain.) Gotth. Schneider	*P. castaneocincta* (Hue) Kistenich & Timdal	460	**MK352116**	**MK352295**	Tanzania	2008	*E. Timdal* 10912 (O)
P. kiiensis	*P. castaneocincta*	3560	**MK352186**	**MK352358**	South Africa	2014	*J. Burrows & E. Timdal* 14280 (O)
P. kiiensis	*P. castaneocincta*	4032	**MK352196**	**MK352367**	Thailand	2012	*P. van den Boom* 47239 (hb. v. d. Boom)
P. kiiensis	*P. castaneocincta*	6743	**MK352243**	**MK352410**	Kenya	2013	*P. Kirika, G. Mugambi & H. T. Lumbsch* 3011 (O)
P. kiiensis	*P. castaneocincta*	7255	**MK352270**	**MK352434**	Australia	1992	*J. A. Elix* 32834 (CANB)
P. loekoesii S.Y. Kondr. *et al.*	N/A	1033	**MK352156**	**MK352331**	Nepal	2007	*L. R. Sharma, L. Olley & A. Cross* C5 (E)
P. loekoesii	N/A	7478	**MK352279**	**MK352439**	Japan	1994	*G. Thor* 12574 (TNS)
P. longiuscula (Nyl.) Zahlbr.	N/A	467	**MK352117**	**MK352296**	Trinidad and Tobago	2008	*S. Rui & E. Timdal* 10730 (O)
P. longiuscula	N/A	1039	**MK352159**	**MK352334**	Cuba	2006	*S. Pérez-Ortega* s.n. (hb. Pérez-Ortega)
P. longiuscula	N/A	6761	MK352246	MK352413	Sri Lanka	2017	*G. Weerakoon* Kn136 (PDA)
P. malcolmii Vězda & Kalb *	N/A	1303	**MK352170**	**MK352344**	New Zealand	1994	*W. Malcolm* in Vězda, *Lich. Rar. Exs*. 200 (GZU)
P. martinii Swinscow & Krog	N/A	489	**MK352129**	**MK352309**	Tanzania	1989	*H. Krog* 3T13/007 (O)
P. martinii	N/A	6740	**MK352242**	**MK352409**	Kenya	2014	*P. Kirika & H. T. Lumbsch* 4087 (O)
P. mauritiana (Taylor) Swinscow & Krog	N/A	487	**MK352128**	**MK352307**	Tanzania	1988	*H. Krog* 2T12/037 (O)
P. mauritiana	N/A	488	–	**MK352308**	Mauritius	1991	*H. Krog & E. Timdal* MAU09/43 (O)
P. mauritiana	N/A	SE386	MG925900	MG925997	Mauritius	1991	*H. Krog & E. Timdal* MAU09/44 (O)
P. mediocris Swinscow & Krog	N/A	527	**MK352144**	**MK352320**	Tanzania	1988	*H. Krog* 2T06/023 (O)
P. mediocris	N/A	6346	**MK352229**	**MK352399**	Mauritius	2016	*P. Diederich* 18571 (hb. Diederich)
P. mediocris	N/A	6347	**MK352230**	**MK352400**	Mauritius	2016	*P. Diederich* 18573 (hb. Diederich)
P. nemoralis Timdal & Krog *	N/A	522	**MK352142**	–	La Réunion	1996	*H. Krog & E. Timdal* RE25/32 (O)
P. nemoralis	N/A	1434	**MK352174**	**MK352347**	South Africa	1996	*A. Nordin* 4622 (UPS:L:92604)

(*Continued*)

TABLE 1 (*continued*).

Species	Revised name	Extract	mtSSU	ITS	Country	Year	Voucher
P. neofoliata Elix	N/A	6745	**MK352244**	**MK352411**	Kenya	2015	*P. Kirika & H. T. Lumbsch* 4728 (O)
P. neofoliata ⋆	N/A	7245	**MK352263**	**MK352429**	Australia	1992	*J. A. Elix* 32714 (O)
P. neofoliata ⋆	N/A	7249	**MK352266**	**MK352432**	Australia	1989	*J. A. Elix* (CANB)
P. ochroxantha (Nyl.) Zahlbr.	N/A	473	**MK352118**	**MK352297**	Peru	2006	*E. Timdal* 10338 (O)
P. ochroxantha	N/A	474	**MK352119**	**MK352298**	Peru	2006	*E. Timdal* 10389 (O)
P. ochroxantha	N/A	475	**MK352120**	**MK352299**	Trinidad and Tobago	2008	*S. Rui & E. Timdal* 10849 (O)
P. ochroxantha	N/A	4049	**MK352206**	**MK352377**	Brazil	2015	*S. Kistenich & E. Timdal* SK1-47 (O)
P. ochroxantha	N/A	4747	**MK352218**	**MK352389**	Brazil	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-289 (O)
P. parvifolia (Pers.) Müll. Arg.	N/A	479	**MK352124**	**MK352303**	Tanzania	2008	*E. Timdal* 10935 (O)
P. parvifolia	N/A	480	**MK352125**	**MK352304**	Trinidad and Tobago	2008	*S. Rui & E. Timdal* 10867 (O)
P. parvifolia	N/A	2049	**MK352181**	**MK352353**	Bolivia	2010	*A. Flakus & J. Quisbert* 20016 (O)
P. parvifolia	N/A	3561	**MK352187**	**MK352359**	South Africa	2014	*J. Burrows & E. Timdal* 14244 (O)
P. parvifolia	N/A	6365	**MK352234**	**MK352402**	Portugal	2015	*P. van den Boom* 53877 (hb. v. d. Boom)
P. parvifoliella (Nyl.) Müll. Arg.	N/A	481	**MK352126**	**MK352305**	Peru	2006	*E. Timdal* 10302 (O)
P. parvifoliella	N/A	482	MG925902	MG925999	Indonesia	2000	*P. A. Wolseley* s. n. (BM:1104069)
P. parvifoliella	N/A	483	MK352127	MK352306	Thailand	1993	*P. W. James & P. A. Wolseley* 2491 (BM)
P. parvifoliella 2	*P. concinna* Kistenich & Timdal	4041	**MK352202**	**MK352373**	Panama	2010	*P. van den Boom* 43947 (hb. v. d. Boom)
P. parvifoliella 2	*P. concinna*	4776	**MK352224**	**MK352395**	Brazil	2015	*M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-445 (O)
P. parvifoliella 2	*P. concinna* ⋆	6455	**MK352236**	**MK352404**	Venezuela	2015	*M. S. Dahl, J. E. Hernández M., S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-225 (O)
P. parvifoliella 2	*P. concinna*	7176	**MK352251**	**MK352418**	Guatemala	2002	*C. Andersohn* s. n. (B)
P. phaeobyssina (Vain.) Timdal	N/A	478	**MK352123**	**MK352302**	Trinidad and Tobago	2008	*S. Rui & E. Timdal* 10872 (O)
P. porphyromelaena (Vain.) Zahlbr. ch1	N/A	498	MG925904	MG926001	La Réunion	1996	*H. Krog & E. Timdal* RE07/17 (O)
P. porphyromelaena ch1	N/A	502	**MK352135**	**MK352314**	Japan	1995	*G. Thor* 12941 (UPS)
P. porphyromelaena ch1	N/A	1050	**MK352164**	**MK352339**	Kenya	2002	*D. Killmann & E. Fischer* s. n. (hb. Killmann)
P. porphyromelaena. ch2	N/A	496	**MK352133**	–	Tanzania	1989	*H. Krog* 4T16/019 (O)
P. porphyromelaena ch2	N/A	503	**MK352136**	**MK352315**	Japan	2006	*G. Thor* 21238 (UPS)
P. porphyromelaena ch2	N/A	7208	MK352255	MK352421	Sri Lanka	2017	*S. Kistenich & G. Weerakoon* SK1-631 (PDA)
P. porphyromelaena ch3	N/A	492	MK352130	MK352310	Thailand	1993	*B. Aguirre, P. W. James & P. Wolseley* 2857 (BM)
P. porphyromelaena ch3	N/A	494	MK352132	MK352312	Thailand	1993	*B. Aguirre, P. W. James & P. Wolseley* 2481 (BM)

(*Continued*)

TABLE 1 (*continued*).

Species	Revised name	Extract	mtSSU	ITS	Country	Year	Voucher
P. pyxinoides (Nyl.) Kistenich *et al.*	*P. gossypina*	GB	AY584615	–	Costa Rica	2002	*R. Lücking* 16052 (DUKE)
P. pyxinoides	N/A	3574	**MK352191**	–	Brazil	2014	*M. Cáceres, R. Haugan & E. Timdal* 21024 (O)
P. pyxinoides	N/A	7358	**MK352274**	–	USA	1991	*B. Ryan* 27530 (O)
P. rappiana (Brako) Elix	N/A	6737	**MK352240**	**MK352407**	Australia	2005	*J. Elix* 36867 (O)
P. rappiana	N/A	7175	**MK352250**	**MK352417**	Panama	2010	*P. van den Boom* 43820 (hb. v. d. Boom)
P. rosei Coppins & P. James	N/A	1299	**MK352168**	–	UK	1992	*B. Coppins, P. W. James & J. Poelt* Sc92/446 (GZU)
P. rosei	N/A	6339	**MK352228**	**MK352398**	France	2000	*P. Diederich* 14602 (hb. Diederich)
P. rosei	N/A	7356	**MK352272**	**MK352436**	France	1990	*P. Diederich* 9247 (hb. Diederich)
P. rosei	N/A	7357	**MK352273**	**–**	UK	1992	*B. Coppins, P. W. James & J. Poelt* Sc92/193 (GZU)
P. santensis (Tuck.) Swinscow & Krog	N/A	2043	**MK352179**	**MK352351**	Bolivia	2009	*A. Flakus & P. Rodriguez* 15581 (O)
P. santensis	N/A	4038	**MK352200**	**MK352371**	Panama	2010	*P. van den Boom* 44704 (hb. v. d. Boom)
P. santensis	N/A	4051	**MK352207**	**MK352378**	Brazil	2015	*S. Kistenich & E. Timdal* SK1-79 (O)
P. sp. 1	*P. amazonica* Kistenich & Timdal	3619	**MK352194**	**MK352365**	Brazil	2014	*R. S. Barbosa, R. Haugan & E. Timdal* 90 (O)
P. sp. 1	*P. amazonica* ⋆	4155	**MK352208**	**MK352379**	Brazil	2015	*S. Kistenich & E. Timdal* SK1-85 (MPEG)
P. sp. 2	N/A	1017	MK352148	–	Malaysia	1997	*P. Wolseley* s. n. (BM:1104019)
P. sp. 3	N/A	7227	MK352258	MK352424	Sri Lanka	2017	*S. Kistenich & G. Weerakoon* SK1-555 (PDA)
P. sp. 4	N/A	7230	MK352259	MK352425	Sri Lanka	2017	*S. Kistenich & G. Weerakoon* SK1-545 (PDA)
P. subhispidula (Nyl.) Kalb & Elix	N/A	501	**MK352134**	**MK352313**	Tanzania	1989	*H. Krog* 4T15/007 (O)
P. subhispidula	N/A	6738	**MK352241**	**MK352408**	La Réunion	1996	*H. Krog & E. Timdal* RE36/15 (O)
P. subhispidula	N/A	6771	MK352249	MK352416	Sri Lanka	2017	*G. Weerakoon* Hg29A (PDA)
P. swinscowii Timdal & Krog	N/A	476	**MK352121**	**MK352300**	Peru	2006	*E. Timdal* 10190 (O)
P. swinscowii ⋆	N/A	525	**MK352143**	–	Mauritius	1991	*H. Krog & E. Timdal* MAU09/50 (O)
P. swinscowii	N/A	1025	**MK352151**	**MK352326**	Cuba	2007	*T. Tønsberg* 37817 (BG)
P. swinscowii	N/A	1049	**MK352163**	**MK352338**	Kenya	2002	*D. Killmann & E. Fischer* s. n. (hb. Killmann)
P. swinscowii	N/A	4048	**MK352205**	**MK352376**	Brazil	2015	*S. Kistenich & E. Timdal* SK1-115 (O)
P. teretiuscula Timdal ⋆	N/A	1026	**MK352152**	**MK352327**	Cuba	2007	*T. Tønsberg* 37814 (BG)
P. teretiuscula	N/A	1306	**MK352171**	**MK352345**	Costa Rica	2003	*Hafellner & Emmerer* 1490 (GZU)
P. teretiuscula	N/A	7474	**MK352278**	**MK352438**	Puerto Rico	1992	*R. C. Harris* 27320 (O)
P. thaleriza (Stirt.) Brako	N/A	1048	**MK352162**	**MK352337**	Kenya	2003	*D. Killmann & E. Fischer* s. n. (hb. Killmann)
P. thaleriza	N/A	5465	MG925880	MG925982	South Africa	2014	*J. Burrows & E. Timdal* 14191 (O)
P. thaleriza	N/A	5466	MG925881	MG925983	South Africa	2015	*S. Rui & E. Timdal* 13877 (O)
P. thaleriza	N/A	5467	**MK352226**	**MK352397**	South Africa	2015	*S. Rui & E. Timdal* 13873 (O)

each run was discarded as burn-in when combining the tree-files using LogCombiner v.2.5.0 as implemented in the BEAST 2 package. We used TreeAnnotator v.2.5.0 (BEAST 2 package) to generate posterior probabilities of nodes from the remaining trees of the combined runs on the maximum clade credibility tree with mean node heights. The resulting tree was edited in TreeGraph2.

Species delimitation analyses

We subjected our datasets to species delimitation analyses to compare our morphological understanding of species with a delimitation based on DNA sequence data. We conducted a PTP (Poisson Tree Processes) analysis using mPTP v.0.2.4 (Zhang *et al.* 2013; Kapli *et al.* 2017) on the mtSSU and ITS gene trees separately, as mPTP handles single-locus data only. This software models speciation by directly using the number of nucleotide substitutions and thus inferring borders of the coalescent process (Zhang *et al.* 2013). We used as input the best tree for each alignment generated by IQ-TREE and conducted both MCMC and maximum likelihood (ML) analyses using both the single- and the multi-rate versions of mPTP. For each MCMC mPTP analysis, we conducted four MCMC runs with 100×10^6 generations, sampling every millionth generation and assessed convergence. The first 10% of the MCMC samples was discarded as burn-in. We compared the results of the single-rate and multi-rate versions using a simple hierarchical likelihood ratio test (hLRT) to examine for overparameterization.

Results

Morphology and secondary chemistry

Species delimitation based solely on morphology proved difficult. While some specimens could be unambiguously identified (e.g. *P. cuyabensis*, *P. halei* and *P. parvifolia*), others had to be re-identified after TLC analysis (e.g. *P. buettneri*, *P. ochroxantha*, *P. porphyromelaena* and *P. swinscowii*). To facilitate morphological species identification, we have provided a table summarizing the main morphological features of each species (see Supplementary Material Table S2, available online). In total, 29 known chemical compounds were identified in species of *Phyllopsora*, in addition to various unidentified terpenoids, xanthones, pigments and other substances (Table 2). Seven species showed intraspecific chemotypic variation, with two new chemotypes recorded for both *P. africana* and *P. porphyromelaena* (Table 2).

Based on our own experience with species identification of *Phyllopsora* using morphology and chemical data we grouped the specimens into 48 morphospecies. Approximately 25% of the total material investigated could not be assigned to any known species.

Molecular data

We selected up to 13 individuals per morphospecies and included five unidentified specimens for DNA extraction and sequencing. We obtained mtSSU and ITS sequences for most *Phyllopsora* species, but only rarely for old (>30 years old) and/or poor quality specimens. In general, specimens collected less than ten years ago performed the best for DNA work, although we also obtained sequences from a specimen collected in 1969 (*P. confusa*; Table 1). The sequencing success was higher for the mtSSU than for the ITS. We produced 153 new mtSSU and 134 new ITS sequences (Table 1). In total, we generated DNA sequence data from 48 out of 64 accepted species (Supplementary Material Table S1, available online), including sequences of 11 types. This study is published along with a revision of the genus *Phyllopsora* in South-East Asia (Kistenich *et al.* 2019*a*), where the additional Asian material of *Phyllopsora* will be treated phylogenetically in detail.

Based on local BLAST searches, the following seven species were found to belong to different *Phyllopsora*-segregates, which were excluded from *Phyllopsora* in Kistenich *et al.* (2018*a*): 1) *Bacidia*-clade: *P. conwayensis* Elix, and 2) *Toninia*-clade: *P. cognata* (Nyl.) Timdal, *P. glaucescens* Timdal, *P. longispora* Swinscow & Krog, *P. pocsii* Vězda, *P. soralifera* Timdal and *P. tobagensis* Timdal. These species were excluded from the subsequent phylogenetic analyses.

Alignment

The mtSSU alignment consisted of 195 accessions and was 854 bp long with 11·8% missing data. The ITS alignment consisted of 174 accessions and was 861 bp long with

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TABLE 2. *Lichen substances detected in* Phyllopsora *species and their chemotypes.*

Part A

Species, chemotype	NONE	ATR	BARB	ARG	NARG	PAN	DPAN	VIC	NVIC	PHY	CPHY	MPS	MNPS	PARV	FUR	MFUR	MHFUR	FPC
africana 1	·	·	·	m	·	·	·	·	·	·	M	·	·	·	·	·	·	·
africana 2	·	·	·	·	·	·	·	·	·	·	·	S	M	·	·	·	·	·
africana 3	·	·	·	±t-m	·	·	·	·	·	·	M	±t-S	S	·	·	·	·	·
amazonica	·	M	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
breviuscula	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
buettneri 1	·	·	·	·	·	M	·	·	·	·	·	·	·	·	·	·	·	·
buettneri 2	·	·	·	·	·	M	·	·	·	M	·	·	·	·	·	·	·	·
buettneri 3	·	·	·	·	·	·	M	·	·	·	·	·	·	·	·	·	·	·
buettneri 4	·	·	·	M	m	·	·	·	·	·	·	·	·	·	·	·	·	·
byssiseda	±	±t-m	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
canoumbrina	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
castaneocincta	·	·	·	·	·	·	·	·	·	·	·	·	·	·	±M	·	·	·
chlorophaea 1	±	±t	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
chlorophaea 2	·	±t	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·
chodatinica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
cinchonarum	·	±t-M	·	·	·	·	·	·	·	·	·	·	·	·	±m	·	·	±t-M
concinna	·	M	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·	·
confusa	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
corallina	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
cuyabensis	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
dolichospora	·	·	·	·	·	·	·	·	·	·	·	·	·	·	m	m-M	m-M	·
fendleri	±	±m	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
foliata	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
foliatella 1	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
foliatella 2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
furfuracea	·	·	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·
furfurella	·	·	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·
glaucella	·	·	·	·	·	·	·	M	M	·	·	·	·	·	·	·	·	·
gossypina 1	·	·	M	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
gossypina 2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
halei 1	·	M	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
halei 2	·	M	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
halei 3	·	M	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
himalayensis	·	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
hispaniolae	·	·	·	M	·	·	·	·	·	·	m	·	·	·	·	·	·	·

(*Continued*)

TABLE 2 (*continued*).

Part A

Species, chemotype	NONE	ATR	BARB	ARG	NARG	PAN	DPAN	VIC	NVIC	PHY	CPHY	MPS	MNPS	PARV	FUR	MFUR	MHFUR	FPC
imshaugii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
isidiosa	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
isidiotyla	·	±	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
kalbii	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
loekoesii	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
longiuscula	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
malcolmii	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
martinii	·	·	·	M	m	·	·	·	·	·	M	·	·	·	·	·	·	·
mauritiana	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
mediocris	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
melanoglauca	·	·	·	·	·	·	·	M	t-m	·	·	·	·	·	·	·	·	·
methoxymicareica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
microdactyla	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
nemoralis	·	m	·	M	·	·	·	·	·	·	·	·	·	·	·	·	·	·
neofoliata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·
neotinica	·	·	·	±M	·	·	·	·	·	·	·	·	·	·	·	·	·	·
ochroxantha	·	·	·	±t-m	±t	·	·	·	·	M	m-M	·	·	·	·	·	·	·
parvifolia	×	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
parvifoliella	·	±t-m	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·	·
phaeobyssina	·	·	·	M	±m	·	·	·	·	·	·	·	·	·	·	·	·	·
porphyromelaena 1	·	·	·	M	m-M	·	·	·	·	·	·	·	·	·	·	·	·	·
porphyromelaena 2	·	·	·	M	·	M	·	·	·	·	·	·	·	·	·	·	·	·
porphyromelaena 3	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
porphyromelaena 4	·	·	·	M	±t-m	·	·	·	·	·	·	·	·	·	·	·	·	·
pyxinoides	·	M	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
rappiana	·	M	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·	·
rosei	·	·	·	M	±m	·	·	·	·	·	·	·	·	·	·	·	·	·
santensis	·	·	·	M	m-S	·	·	·	·	·	·	·	·	·	·	·	·	·
subhispidula	·	t	·	M	m	·	·	·	·	·	·	·	·	·	·	·	·	·
swinscowii	·	·	·	·	·	·	·	·	·	·	·	m-M	M	·	·	·	·	·
teretiuscula	·	·	·	M	±t-m	·	·	·	·	·	±t-m	·	·	·	·	·	·	·
thaleriza	·	t-m	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·

(Continued)

TABLE 2 (*continued*).

Part B

Species, chemotype	NOR	STIC	LOB	NLOB	PHYS	HSEK	HHSEK	DIV	SAL	HMIC	MMIC	SECA	ZEO	TERP	XAN	PIGM	UNKN
africana 1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
africana 2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
africana 3	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
amazonica	·	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·
breviuscula	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
buettneri 1	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·	·
buettneri 2	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·	·
buettneri 3	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·	·
buettneri 4	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·	·
byssiseda	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
canoumbrina	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
castaneocincta	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
chlorophaea 1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
chlorophaea 2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
chodatinica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·
cinchonarum	·	·	±M	±m	·	·	·	·	·	·	·	±M	·	·	·	±m	±m
concinna	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
confusa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
corallina	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
cuyabensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
dolichospora	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
fendleri	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
foliata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
foliatella 1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
foliatella 2	·	·	·	·	·	M	M	·	·	·	·	·	·	·	·	·	·
furfuracea	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
furfurella	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
glaucella	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
gossypina 1	·	·	·	·	·	·	·	S	·	·	·	·	·	m	·	·	·
gossypina 2	M	·	·	·	·	·	·	·	±M	·	·	·	·	·	·	·	t-m
halei 1	·	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·
halei 2	·	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·
halei 3	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	M
himalayensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
hispaniolae	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·

(*Continued*)

TABLE 2 (*continued*).

Part B

Species, chemotype	NOR	STIC	LOB	NLOB	PHYS	HSEK	HHSEK	DIV	SAL	HMIC	MMIC	SECA	ZEO	TERP	XAN	PIGM	UNKN
imshaugii	M	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
isidiosa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
isidiotyla	·	·	·	·	·	·	·	·	·	·	·	·	±	·	·	·	·
kalbii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
loekoesii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
longiuscula	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
malcolmii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
martinii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
mauritiana	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
mediocris	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
melanoglauca	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·	·
methoxymicareica	·	·	·	·	·	·	·	·	·	t	M	·	·	·	·	·	·
microdactyla	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
nemoralis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
neofoliata	·	·	·	·	±t-m	·	·	·	·	·	·	·	·	·	·	·	·
neotinica	·	·	·	·	·	·	·	·	·	·	·	·	±t-m	·	M	·	·
ochroxantha	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	±t
parvifolia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
parvifoliella	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
phaeobyssina	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
porphyromelaena 1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
porphyromelaena 2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
porphyromelaena 3	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·	M
porphyromelaena 4	·	·	·	·	·	·	·	·	·	·	·	·	t-m	·	·	·	·
pyxinoides	·	M	·	·	·	·	·	·	·	·	·	·	·	t-m	·	·	·
rappiana	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
rosei	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
santensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
subhispidula	·	·	·	·	·	·	·	·	·	·	·	·	M	·	·	·	·
swinscowii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
teretiuscula	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
thaleriza	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·

NONE: no lichen substances, ATR: atranorin, BARB: barbatic acid, ARG: argopsin, NARG: norargopsin, PAN: pannarin, DPAN: dechloropannarin, VIC: vicanicin, NVIC: norvicanicin, PHY: phyllopsorin, CPHY: chlorophyllopsorin, MPS: methyl 2,7-dichloropsoromate, MNPS: methyl 2,7-dichloronorpsoromate, PARV: parvifoliellin, FUR: furfuraceic acid, MFUR: methyl furfuraceiate, MHFUR: methyl homofurfuraceiate, FPC: fumarprotocetraric acid, NOR: norstictic acid, STIC: stictic acid, LOB: lobaric acid, NLOB: norlobaric acid, PHYS: physodic acid, HSEK: homosekikaic acid, HHSEK: hyperhomosekikaic acid, DIV: divaricatic acid, SAL: salazinic acid, HMIC: hydroxymicareic acid, MMIC: methoxymicareic acid, SECA: secalonic acid A, ZEO : zeorin, TERP: terpenoids, XAN: xanthones, PIGM: pigments, UNKN: unknown compounds.
M = major; S = submajor; m = minor; t = trace; x = present; ± = present or absent

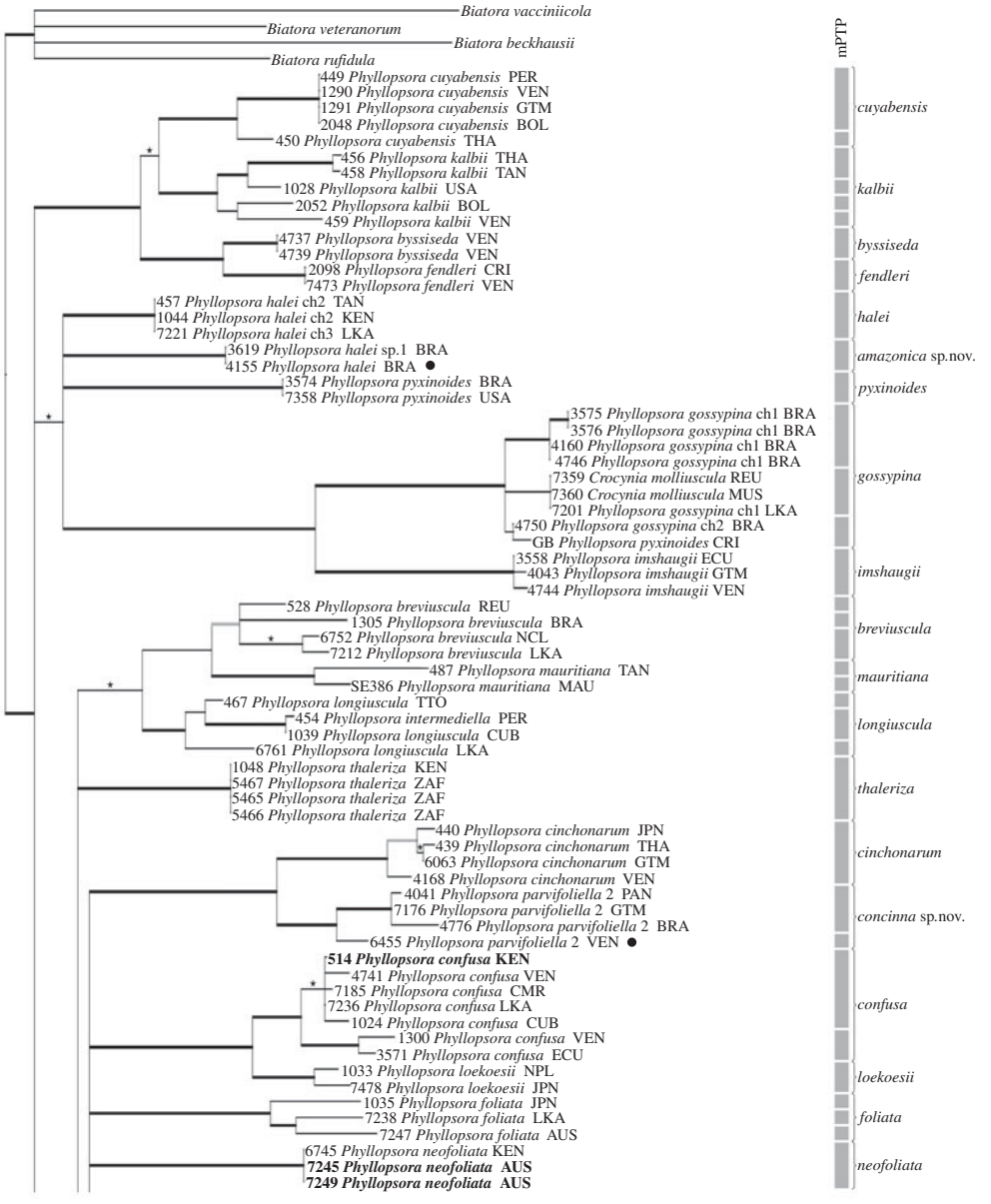

FIG. 2. mtSSU molecular phylogenetic tree. Extended majority-rule consensus tree resulting from the IQ-TREE analysis of the mtSSU alignment with Bayesian PP ≥ 0·7 and/or IQ-TREE maximum likelihood BS ≥ 50 and branch lengths. Strongly supported branches (PP ≥ 0·95 and BS ≥ 70) are marked in bold; branches with PP ≥ 0·95 and BS < 70 or PP < 0·95 and BS ≥ 70 are marked in bold grey; branches supported only with PP ≥ 0·7 or BS ≥ 50 are marked with an asterisk above the branch. Four species of *Biatora* were used for rooting. Accessions in bold indicate sequences of type specimens; black dots indicate sequences of type specimens for those species described here as new. All accession names include the official three-letter country codes according to ISO 3166-1 alpha-3. The species delimitation results of the mPTP analysis are indicated on the right, including the revised species understanding as of this study. Three major groups are distinguished to facilitate discussion (A, B, C). ch = chemotype. The numbers preceding the names are extract numbers for reference (Table 1).

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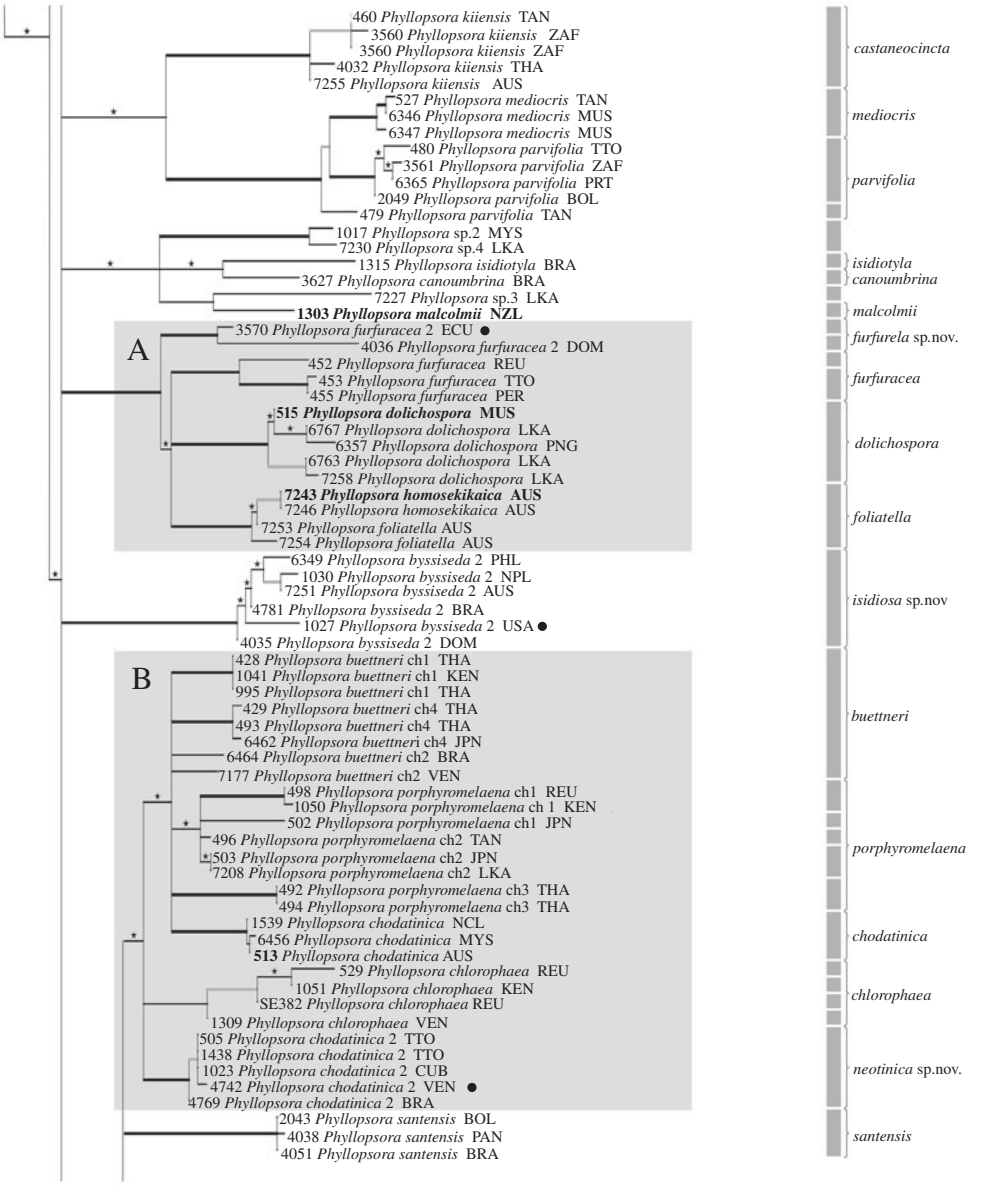

FIG. 2 (*continued*).

10·9% missing data. Both alignments are available from TreeBase (study no. 23741).

Model selection

The software IQ-TREE reported the GTR+I+Γ model as the best-fitting substitution model for the mtSSU alignment. For ITS, the software reported the following models and partitioning schemes: GTR+I+Γ for ITS1 and ITS2 separately, SYM+I+Γ for 5.8S and GTR+I+Γ for the entire ITS region. For the *BEAST analysis, IQ-TREE reported the GTR+I+Γ model as the

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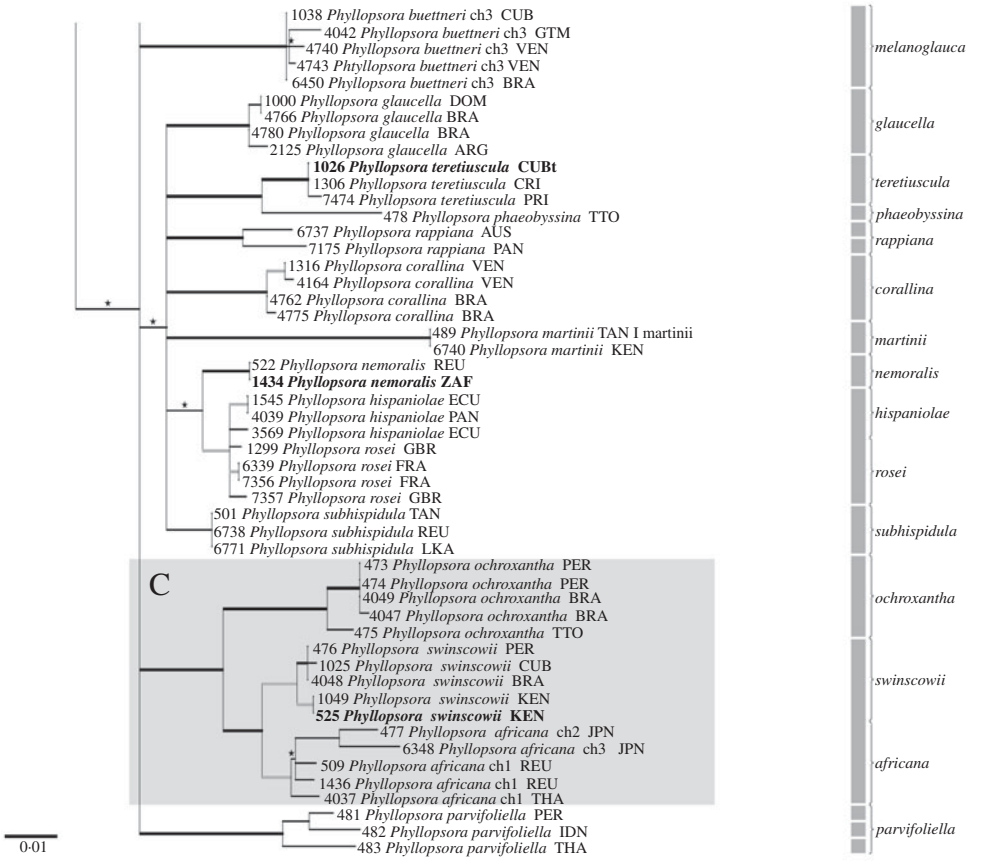

FIG. 2 (*continued*).

best-fitting substitution model for both the mtSSU and ITS alignments.

Phylogenetic analysis of separate markers

The software compat.py reported several incongruences between the two gene trees generated by IQ-TREE. Most of these incongruences involved subterminal branches within one species but no strongly supported topological differences in the backbone. We chose not to concatenate our datasets due to these incompatibilities.

The MrBayes analyses halted automatically, after 11×10^6 generations for the mtSSU alignment and after 12×10^6 generations for the ITS alignment, when the ASDSF in the last 50% of each run had fallen below 0·01. We used 22 004 trees from the mtSSU analysis and 24 004 trees from the ITS analysis for constructing each final majority-rule consensus tree. Overall, the mtSSU tree showed a better resolution than the ITS tree. In general, accessions belonging to the same predefined morphospecies grouped together in both gene trees but, when resolved, relationships between morphospecies were slightly different between gene trees. In total, five morphospecies (i.e. *P. buettneri*, *P. byssiseda*, *P. chodatinica*, *P. furfuracea* and *P. parvifoliella*) proved polyphyletic and fell into two different clades each in both trees (Figs 2 & 3). Two of the five unidentified specimens

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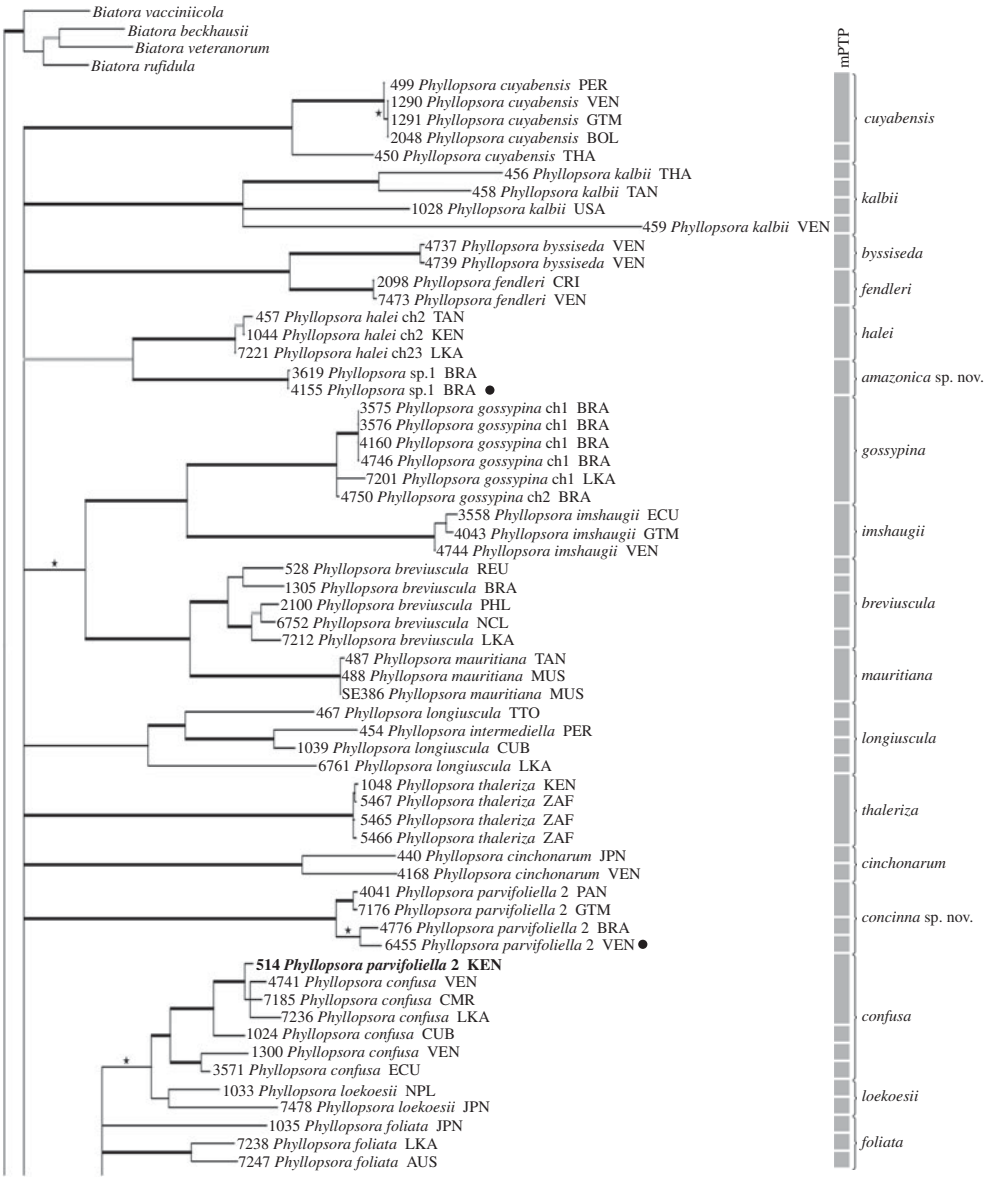

FIG. 3. ITS molecular phylogenetic tree. Extended majority-rule consensus tree resulting from the IQ-TREE analysis of the ITS alignment with Bayesian PP ≥ 0·7 and/or IQ-TREE maximum likelihood BS ≥ 50 and branch lengths. Strongly supported branches (PP ≥ 0·95 and BS ≥ 70) are marked in bold; branches with PP ≥ 0·95 and BS < 70 or PP < 0·95 and BS ≥ 70 are marked in bold grey; branches supported only with PP ≥ 0·7 or BS ≥ 50 are marked with an asterisk above the branch. Four species of *Biatora* were used for rooting. Accessions in bold indicate sequences of type specimens; black dots indicate sequences of type specimens for those species described here as new. All accession names include the official three-letter country codes according to ISO 3166-1 alpha-3. The species delimitation results of the mPTP analysis are indicated on the right, including the revised species understanding as of this study. Three major groups are distinguished to facilitate discussion (A, B, C). ch = chemotype. The numbers preceding the names are extract numbers for reference (Table 1).

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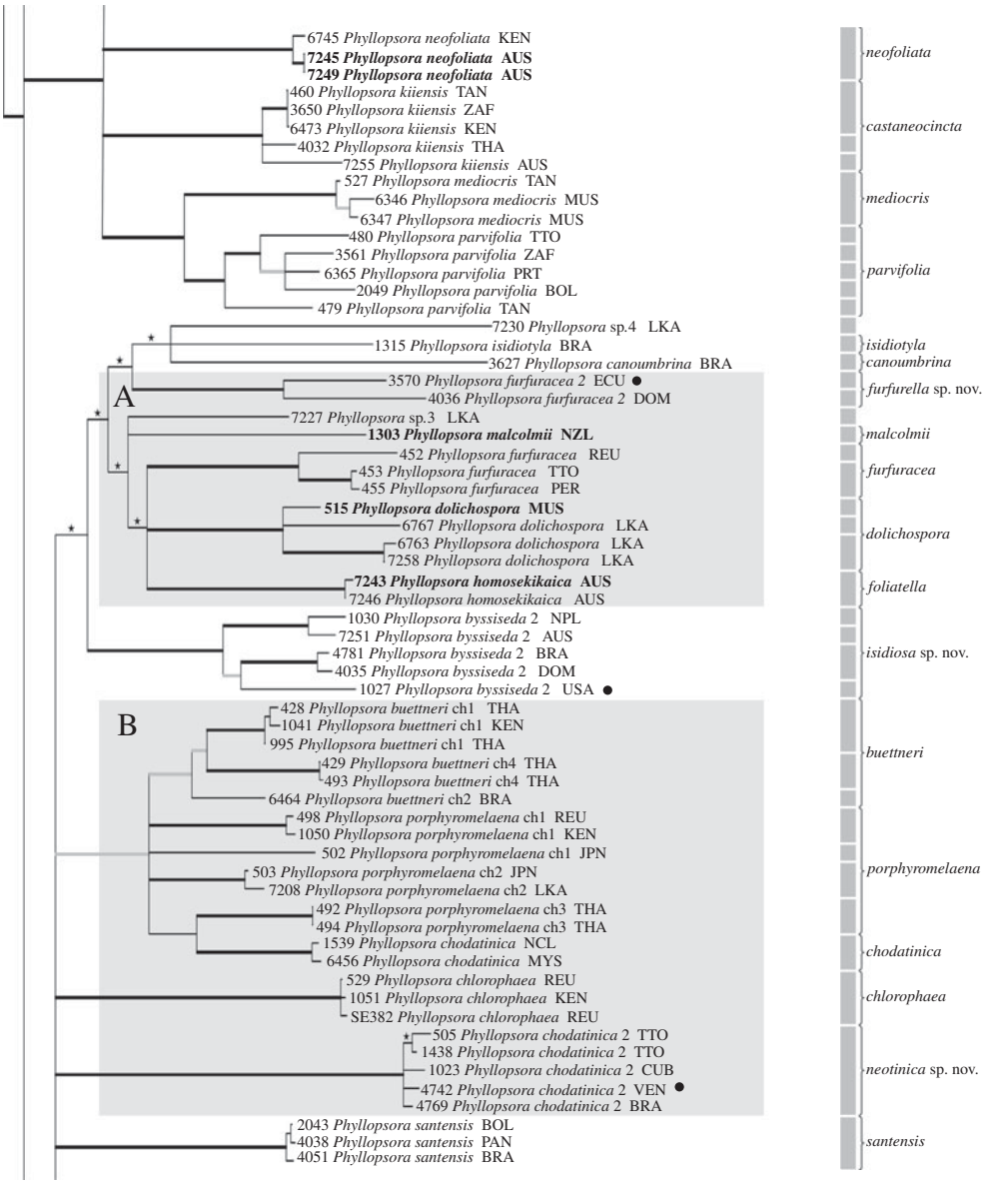

FIG. 3 (*continued*).

grouped closely together as sister to *P. halei*, while the remaining three only showed a weakly supported relationship with *P. canoumbrina*, *P. isidiotyla* and *P. malcolmii*, respectively, and sit on long branches (Figs 2 & 3). Both trees showed three occasions where accessions of different predefined morphospecies mixed with another: *P. hispaniolae* and *P. rosei*, *P. homosekikaica* and *P. foliatella* as well as *P. buettneri*, *P. porphyromelaena* and *P. chodatinica* (Figs 2 & 3). We indicate three groups of species complexes to facilitate discussion (Figs 2 & 3, groups A–C).

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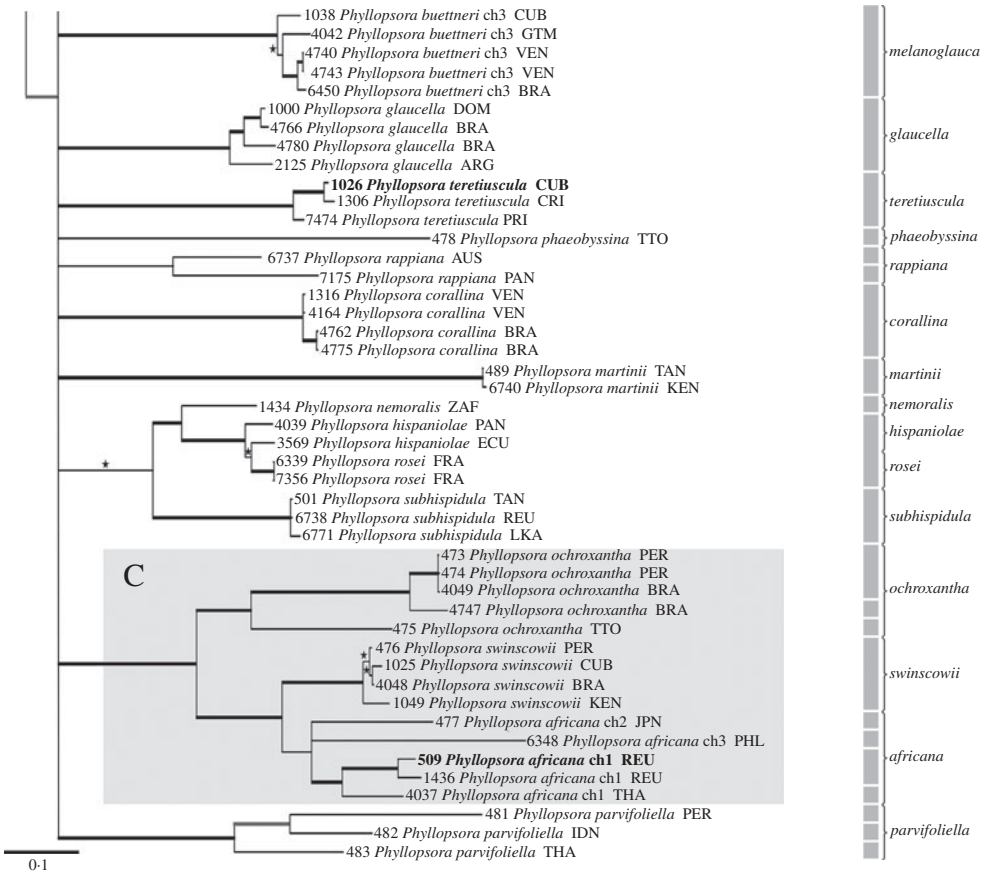

FIG. 3 (*continued*).

Species delimitation analysis

According to the hLRT, the single-rate version of mPTP was preferred over the multi-rate version for each gene tree ($P > 0{\cdot}01$) and only the results of the single-rate version are presented here. The single-rate version of mPTP reported 79 delimited species for the mtSSU tree and 96 for the ITS tree. Results from the MCMC analyses were identical to the results from the ML analyses. In the single-rate analyses of each dataset, splitting morphological species was more common than lumping, and species were more often split in the ITS analysis (Figs 2 & 3). In general, long branches increased the frequency of inferring a species boundary in mPTP. *Phyllopsora buettneri* and *P. porphyromelaena* were divided into several species, partly according to chemotypes (Figs 2 & 3). The accessions of *P. foliatella* and *P. homosekikaica* as well as *P. hispaniolae* and *P. rosei* were delimited as only one species each (Figs 2 & 3).

Species tree reconstruction

For the species tree reconstruction with *BEAST, we used 160 004 trees to construct the maximum clade credibility tree (Fig. 4). The species tree does not show higher resolution than the gene trees (Figs 2 & 3) and is largely concordant with those. The phylogenetic placement of *P. furfurella* differs in the mtSSU and ITS trees (Figs 2 & 3), and the species is resolved here as sister to *P. dolichospora*, *P. foliatella* and *P. furfuracea* (Fig. 4). In the species tree, group B is resolved as a strongly supported clade (Fig. 4).

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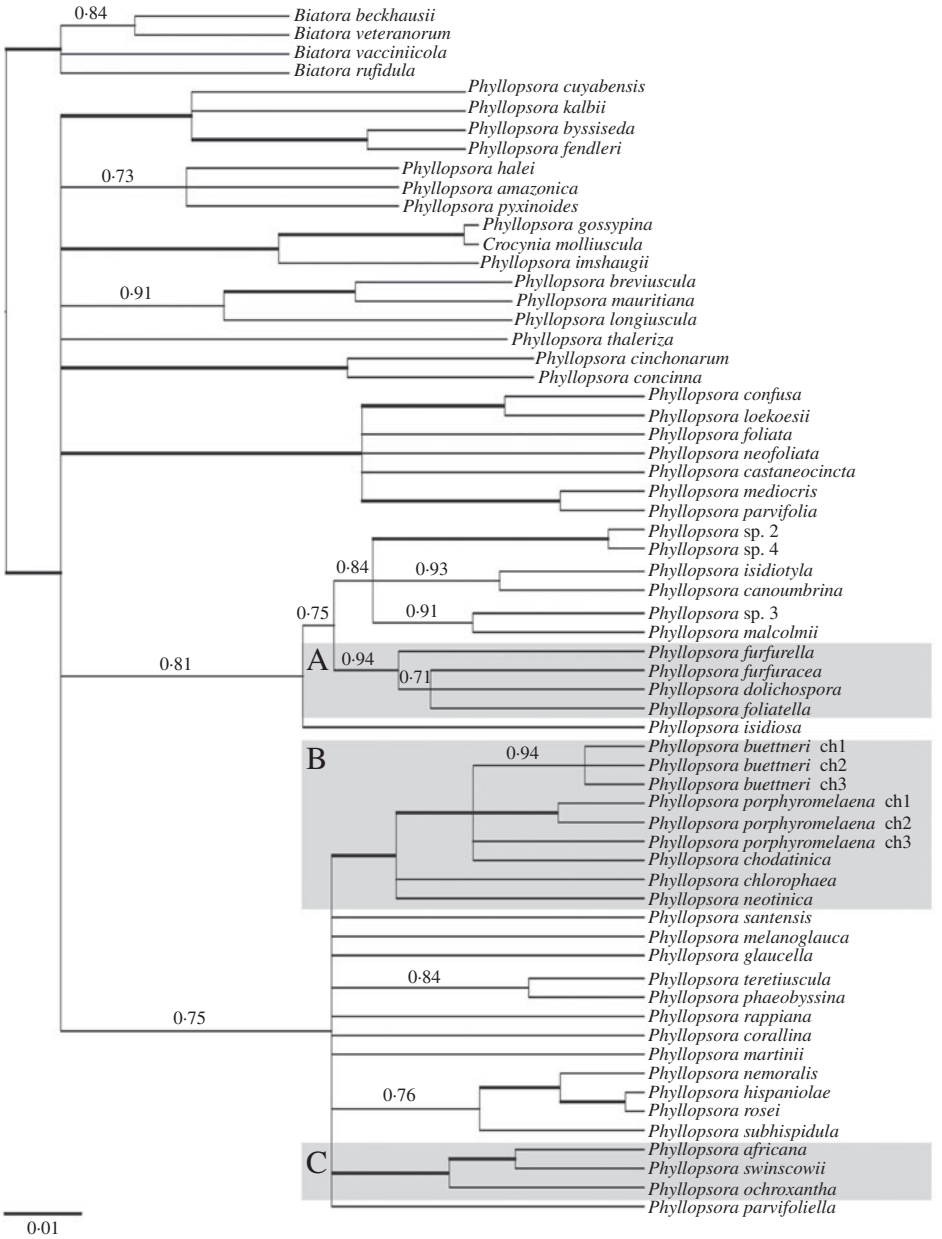

FIG. 4. Species tree reconstruction with a maximum clade credibility tree resulting from the *BEAST analysis of the combined mtSSU and ITS data with PP ≥ 0·7 and branch lengths. Strongly supported branches with PP ≥ 0·95 are marked in bold; PP values are given for PP ≤ 0·95. Four species of *Biatora* were used for rooting. Three major groups are distinguished to facilitate discussion (A, B, C). The classification is based on the revised taxonomy of accepted *Phyllopsora* species. ch = chemotype.

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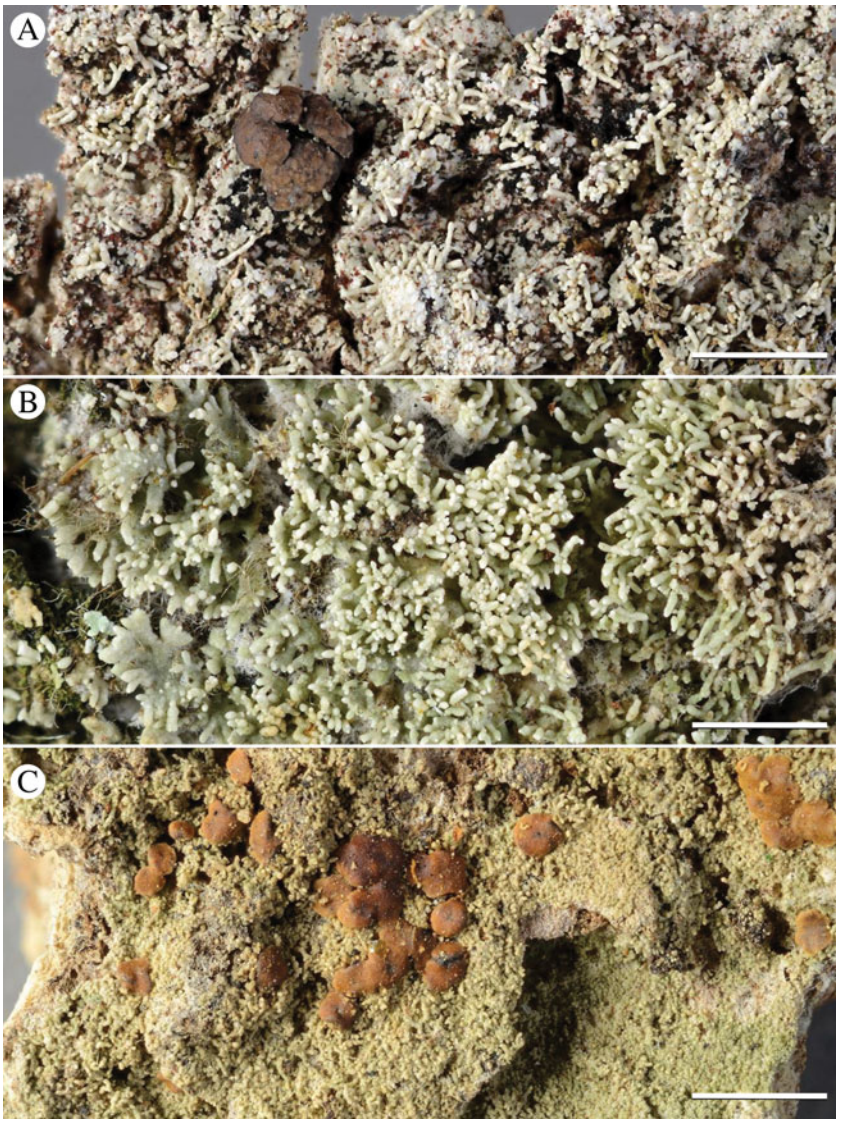

FIG. 5. Habit of *Phyllopsora* species described here as new: A, *P. amazonica* (O L-201094); B, *P. concinna* (O L-202505); C, *P. furfurella* (HUTPL, M. Prieto). Scales: A–C = 2 mm. In colour online.

Taxonomic conclusions

As a result of the phylogenetic and species delimitation analyses, the species *P. melanoglauca* is resurrected for *P. buettneri* chemotype 3, and the species *P. amazonica* ('*Phyllopsora* sp.1'; Fig. 5A), *P. concinna* ('*P. parvifoliella* 2'; Fig. 5B), *P. furfurella* ('*P. furfuracea* 2'; Fig. 5C), *P. isidiosa* ('*P. byssiseda* 2'; Fig. 6A) and *P. neotinica* ('*P. chodatinica* 2'; Fig. 6B) are described as new. *Phyllopsora homosekikaica* is synonymized with *P. foliatella*, and *P. intermediella* is synonymized with *P. longiuscula*.

Discussion

In this study, we provide a comprehensive contribution to the much needed revisionary work

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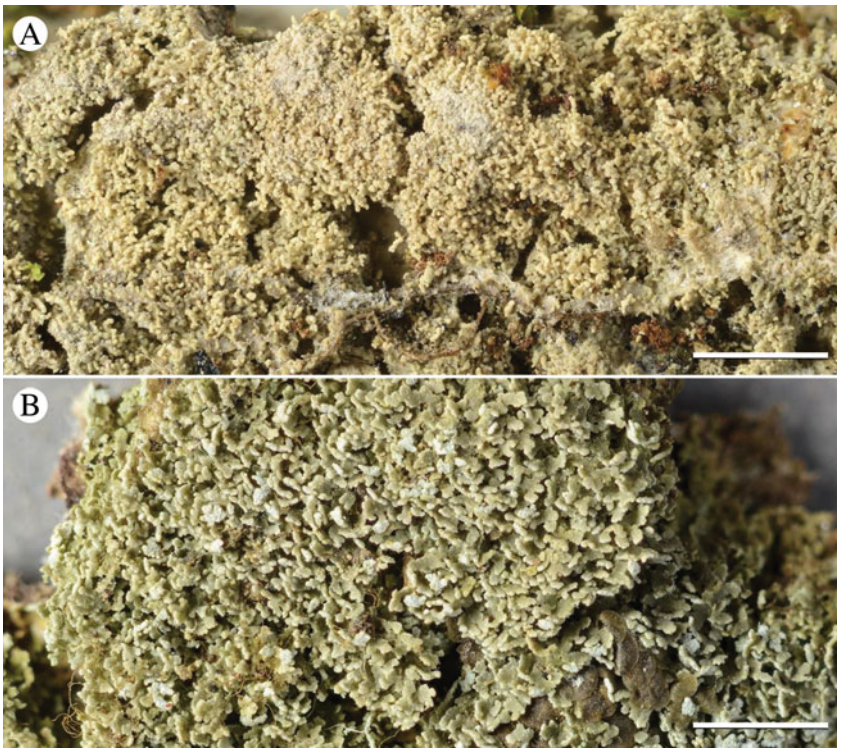

FIG. 6. Habit of *Phyllopsora* species described here as new: A, *P. isidiosa* (BG L-93867); B, *P. neotinica* (O L-202526). Scales: A & B = 2 mm. In colour online.

of the current *Phyllopsora* taxonomy. As species of *Phyllopsora* are generally difficult to identify based on morphology and chemistry only, molecular data give a new perspective on species circumscriptions in this mainly tropical genus. Based on our multiple sources of data, we describe five new species (i.e. *P. amazonica*, *P. concinna*, *P. furfurella*, *P. isidiosa* and *P. neotinica*), resurrect *P. melanoglauca*, and synonymize *P. homosekikaica* with *P. foliatella* and *P. intermediella* with *P. longiuscula*.

Species circumscriptions in *Phyllopsora*

In most cases accessions of the same species grouped together in well-supported clades on the molecular phylogenetic trees (Figs 2 & 3), supporting our traditional understanding of the species boundaries. This indicates that a detailed analysis of morphological characters in combination with patterns of lichen substances lay a useful foundation for species delimitation in *Phyllopsora*. Due to numerous incongruences in more ancestral and/or terminal nodes, we did not concatenate the mtSSU and ITS alignments, but decided to run a *BEAST analysis to obtain a species tree (Fig. 4). The gene trees taken together provide valuable information about species limits and indicate the extent of morphological and chemical character variation in each species. The species tree, in turn, informs us about relationships among *Phyllopsora* species. Detailed discussions of each accepted species are provided in the Taxonomy section, part A.

Morphological characters used to delimit *Phyllopsora* species mainly include thallus structure, texture and colour of the prothallus, presence or absence and type of

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vegetative dispersal units, as well as ascospore anatomy including spore dimensions (Timdal & Krog 2001). Even with experience in identifying *Phyllopsora* specimens, species identification using only morphological features is usually time-consuming and often unreliable. Many of the specimens investigated had to be renamed more than once after tentative identification by morphology, then chemistry and subsequently DNA sequence data. Not surprisingly, many herbarium specimens were incorrectly identified. This shows that new country reports for species of *Phyllopsora* cannot automatically be accepted, especially when TLC has not been performed. Herein, we therefore rely solely on our own species determinations and well-documented species records for mapping geographical species occurrences.

In general, we could observe that most morphological features used to characterize a species, such as vegetative dispersal units, may be found in a variety of not necessarily closely related species. Almost all *Phyllopsora* species seem to exhibit some form of vegetative dispersal structure. Isidia, lacinules and phyllidia seem to have evolved several times and have transformed frequently, rendering them of little use for predicting relationships among *Phyllopsora* species and evolutionary lineages therein: while some clades of sister species seem to be consistent in their means of vegetative dispersal, other clades seem to have switched the preferred dispersal units. Lacinules are found in a small number of closely related species (e.g. in the *buettneri-chlorophaea-chodatinica-porphyromelaena* group; Figs 2–4, group B), whereas isidia are the most common means of vegetative dispersal. They are observed in the *dolichospora-foliatella-furfuracea* group (Figs 2–4, group A), the *africana-ochroxantha-swinscowii* group (Figs 2–4, group C) as well as in numerous other species, such as *P. cinchonarum*, *P. corallina*, *P. glaucella* and *P. rappiana*. Within some clades (Figs 2–4), on the other hand, closely related species may form different vegetative dispersal propagules, for example, in the *mediocris-parvifolia* clade (lacinules and phyllidia) or the *confusa-loekoesii* clade (lacinules and isidia). We also found that different types of vegetative diaspores might be present on different specimens of the same species, such as in *P. africana* (isidiate and lacinulate morphs) and *P. longiuscula* (isidia or lacinules; the isidiate morph, previously named *P. intermediella*, being synonymized here). In other species previously not known to produce isidia, such as *P. fendleri*, we observed a few but distinct isidia. Previously Brako (1991: 7) suggested that the presence or absence of isidia was an unreliable character for identification of most species.

TLC analysis of lichen substances is often crucial for correct species identification in *Phyllopsora*. Some chemical compounds are not known to occur outside the genus, such as furfuraceic acid, parvifoliellin and phyllopsorin. In total, we identified 29 lichen compounds in addition to various pigments, terpenoids, xanthones and unidentified compounds throughout *Phyllopsora*, as circumscribed in this article (Table 2). About 30% of the species did not contain any lichen substances. We observed similar patterns in the distribution of lichen substances between species as in the distribution of vegetative dispersal units. Certain lichen substances are found both within and outside of groups of species complexes (Table 2). Furfuraceic acid, for example, is present in the species of the *furfuracea-dolichospora* group (Figs 2–4, group A), as well as in *P. castaneocincta*, *P. chlorophaea* and *P. neofoliata*; chlorophyllopsorin is present in the *africana-ochroxantha* group (Figs 2–4, group C) but also in *P. hispaniolae*, *P. martinii* and *P. teretiuscula*. Several *Phyllopsora* species are known to comprise different chemotypes, such as *P. buettneri* and *P. porphyromelaena*, including species with acid-deficient strains, such as *P. foliatella* (Table 2). In the latter, we found specimens with a rather complex chemistry (hyperhomosekikaic and homosekikaic acids) but also specimens lacking substances. We assume that the loss of chemical substances has been more common than switching to chemically unrelated substances, as previously suggested by Culberson & Culberson (2001). The presence of acid-deficient chemotypes is similarly found in *P. castaneocincta* but does not generally seem to be a common phenomenon in *Phyllopsora* species.

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Species showing distinct morphological characters (e.g. *P. cuyabensis*) or a unique composition of lichen substances (e.g. *P. dolichospora*) are readily identifiable. Poorly developed morphotypes and/or acid-deficient strains, however, are far more challenging to identify. In these cases, DNA sequence data seem to be necessary to reliably identify the specimens. We found either genetic marker to be suitable for species identification, although the mtSSU tree was slightly more resolved than the ITS tree (Figs 2 & 3). Molecular species identification, however, may be ambiguous when no reference sequences exist or species clades are poorly resolved. The use of a fixed barcode gap has been suggested to facilitate species circumscription (Hebert *et al.* 2003; Schoch *et al.* 2012). The gene trees showed that the molecular differences found within and between species based on branch lengths are highly variable (Figs 2 & 3). Many clades have only short intraspecific branches (e.g. *P. corallina*, *P. glaucella* and *P. melanoglauca*) while others are longer (e.g. *P. kalbii* and *P. longiuscula*; Figs 2 & 3). This indicates that a fixed barcode gap cannot be applied here, based on the genetic markers and *Phyllopsora* species circumscriptions used. Instead, each case has to be evaluated separately.

Unresolved species complexes

Most of our predefined morphospecies each grouped into a supported clade in the gene trees (Figs 2 & 3). However, some groups of species could not be fully resolved by mtSSU or ITS and require further attention in future studies. Sequencing additional markers, as well as increasing the sample size with specimens from additional geographical regions, will most likely provide improved resolution for delimiting the problematic species.

One of the species complexes that was not fully resolved is group B (Figs 2–4). We found several morphologically identical chemotypes (Table 2) in both *P. buettneri* and *P. porphyromelaena* (Timdal 2011). We were curious to investigate whether these represent species with chemical variation or include several distinct, yet morphologically inseparable taxa. In the case of *P. buettneri*, we sampled specimens from four out of five described chemotypes and recovered them according to chemotypes in the two gene trees (Figs 2 & 3). Chemotype 3, present in South America, was resolved as a separate species outside group B (Figs 2 & 3). This chemotype was originally described as a separate species, *P. melanoglauca* Zahbr., but was reduced into synonymy with *P. buettneri* in two steps; first by Brako (1991) who treated it as a variety of *P. buettneri*, and then by Timdal (2008). As it is phylogenetically distinct from the morphologically identical *P. buettneri*, we resurrect the species *P. melanoglauca* (see also section on new species below). The other three chemical strains of *P. buettneri* grouped with varying support (Figs 2 & 3). Chemotypes 1 and 4 are currently known from the Palaeotropics, chemotype 2 from the Neotropics and chemotype 5 (not examined by us) from Australia (Elix 2006*b*). The mPTP analysis resolved chemotypes 1, 2 and 4 as separate species on the ITS tree (Fig. 3), while they grouped into a single species on the mtSSU tree (Fig. 2), probably because the mtSSU is too conserved to distinguish among chemotypes. Our accessions of *P. porphyromelaena* were also resolved according to chemotype, albeit with less support than in *P. buettneri*. We also found two new chemical strains (chemotypes 3 and 4) in *P. porphyromelaena*. Chemotype 3 is present in Thailand, but its accessions cluster with *P. chodatinica* instead of the other *P. porphyromelaena* specimens and are resolved as a separate species in both mPTP analyses (Figs 2 & 3). Chemotype 4 of *P. porphyromelaena* occurs in the Neotropics. It is identical to chemotype 1 but additionally contains zeorin. Unfortunately, we were not able to obtain sequences of the investigated specimens of chemotype 4. The overall resolution of group B, containing *P. buettneri*, *P. chodatinica* and *P. porphyromelaena* among others, is poor (Figs 2–4). The three species exhibit slightly different thallus morphologies (mean squamule size and pruinosity), spore sizes and chemistry (Elix 2006*a*, *b*, *c*; Table 2). Even though they are morphologically similar, they vary greatly in

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their chemical compositions. Brako (1991) described several chemical strains of the three varieties of *P. buettneri*, which Timdal (2008, 2011) recognized as the chemotypes of three distinct species, *P. buettneri*, *P. chodatinica* and *P. porphyromelaena*. Even when using sequence data from two genetic markers, we were unable to resolve these species and chemotypes.

In contrast to the *buettneri-chodatinica-porphyromelaena* complex, the clade, consisting of *P. africana*, *P. ochroxantha* and *P. swinscowii*, is well delimited on our phylogenetic trees (Figs 2–4, group C) but proved to be more challenging with respect to species delimitation based on morphological and chemical characters. Prior to this study, the three species were regarded as morphologically similar (forming medium-sized, isodiametrical squamules with long, cylindrical isidia and growing on a well-developed reddish brown prothallus) but could be distinguished by chemical composition (argopsin and chlorophyllopsorin, phyllopsorin and chlorophyllopsorin, and methyl 2,7-dichloropsoromate and methyl 2,7-dichloronorpsoromate, respectively; Timdal & Krog 2001; Timdal 2008, 2011). They also exhibit different distribution ranges: *Phyllopsora africana* seems to be present in Asia and Africa, *P. ochroxantha* in South America, and *P. swinscowii* in Africa and South America. Our phylogenies show that the species indeed form a monophyletic group (Figs 2–4, group C). However, relying on chemical patterns for species delimitation has now become more difficult with additional chemotypes described for *P. africana* and sequencing seems to be necessary to assign problematic specimens correctly to either *P. africana* or *P. swinscowii*. However, *P. ochroxantha* may still be distinguished from the other two species by its unique chemistry (Table 2). On the ITS tree, the accession of *P. ochroxantha* from Trinidad and Tobago is separated from the remaining *P. ochroxantha* accessions from Brazil (Fig. 3) by a long branch. This accession might represent a new species but more sequence data from different genetic markers are necessary to determine its status. *Phyllopsora africana* and *P. swinscowii* are more closely related to each other than either is to *P. ochroxantha* (Figs 2–4, group C) and were resolved as a single species in the mtSSU mPTP analysis (Fig. 2). The two psoromate lichen substances, previously characteristic for *P. swinscowii*, were also found in some specimens of *P. africana*. Here we show that *P. africana* forms three different chemotypes: chemotype 1 is found in the holotype of *P. africana*; chemotype 2 is identical to the chemical pattern found in *P. swinscowii*; chemotype 3 represents a combination of 1 and 2 (Table 2). Moreover, the specimens with chemotypes 1 and 3 may also form lacinules instead of isidia. The *P. africana* specimens of chemotype 2 are morphologically identical to *P. swinscowii* and thus the two currently represent a closely related pair of cryptic species (Struck *et al.* 2018). Therefore, *P. africana* seems to be a heterogeneous assemblage of specimens with regard to chemistry and morphology, and difficult to delimit from *P. swinscowii*. More sequence data from different markers and from additional specimens are necessary to provide more robust information about whether the new circumscription of *P. africana* (with different chemo- and morphotypes) comprises a good species, or whether it should be synonymized with *P. swinscowii,* or split into several species. Detailed population genetic studies from different parts of the Palaeotropics might improve our knowledge about its taxonomic status.

Another unresolved species complex is the *P. hispaniolae-rosei* complex (Figs 2 & 3). The two species are morphologically different: *P. rosei* forms a granulose thallus on a white prothallus and has 1–3-septate ascospores, while *P. hispaniolae* forms coralloid squamules on a reddish brown prothallus and has simple ascospores. They also differ in their lichen substances (Table 2) and have different distribution ranges, with *P. rosei* being a temperate and *P. hispaniolae* a tropical species. Hence, we suggest keeping the two species separate until further specimens and genetic markers have been examined.

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Kistenich *et al.* (2018*a*) included two species of *Crocynia* in *Phyllopsora*. Previously *Crocynia* was accepted as a distinct genus based on its characteristic cobwebby, byssoid thallus lacking an upper cortex (e.g. Hue 1909, 1924). Many species have been assigned to this genus, most of which are expected to be reassigned to other genera, such as *Lepraria* Ach. The present study corroborates the findings of Kistenich *et al.* (2018*a*) that *Crocynia gossypina* and *C. pyxinoides* indeed belong to *Phyllopsora* (Figs 2–4). Although their clade is not fully resolved, the two species do not group together (Figs 2 & 4), indicating that they are not sister species. Unfortunately, we were only able to generate mtSSU sequences of *P. pyxinoides*. The accession of *P. pyxinoides* downloaded from GenBank seems to be misidentified, as it groups together with the various chemotypes of *P. gossypina* and not with the other two *P. pyxinoides* accessions in the mtSSU tree (Fig. 2). The accessions of *P. gossypina* also group together with a third species of *Crocynia*, *C. molliuscula*, in the mtSSU tree (Fig. 2). The latter differs clearly from *P. gossypina* in forming bright brown, convex, nonmarginate apothecia instead of dark brown apothecia with a lighter margin. Both species overlap in their chemistry by containing norstictic acid, as found in *P. gossypina* chemotype 2 (Table 2). Surprisingly, these species group into one clade with rather short branches (Fig. 2) but a possible synonymy of the two species is difficult to comprehend based on morphology. As we only generated short mtSSU sequences of two *C. molliuscula* specimens, we recommend sequencing additional specimens and providing ITS sequences before drawing taxonomic conclusions. From a morphological point of view, one would have expected species of *Crocynia* to group with *P. cuyabensis*, a species also lacking an upper cortex, but neither species did (Figs 2–4). Our results indicate that the upper cortex has been lost more than once within *Phyllopsora* and is not a reliable criterion for distinguishing *Crocynia*. As *Crocynia* (priority 1860) is an older name, *Phyllopsora* is proposed for conservation (Kistenich *et al.* 2019*b*).

Species delimitation with mPTP

When comparing results generated by the single- and multi-rate models of mPTP, we found that the single-rate model split species more often (Figs 2 & 3), while the multi-rate model lumped several morphologically well-distinguished species into one entity (data not shown). Kapli *et al.* (2017) found the multi-rate model to outperform the single-rate model on a variety of different datasets. In our datasets, however, the hLRT preferred the single-rate model, indicating that the multi-rate model constituted an overparameterization. The single-rate model delimited 3–4 times more entities than the multi-rate version, which is indeed a huge difference and shows the necessity for conducting an hLRT. However, the results generated by both multi-rate and single-rate models seemed to under- and overestimate the correct number of species, respectively. The most reasonable number of species probably lies somewhere in between the two models. Due to this huge difference in delimited entities, we set out to perform a second kind of species delimitation analysis using the software BPP v.4.0 (Bayesian Phylogenetics and Phylogeography; Yang 2015; Flouri *et al.* 2018) for a combined species tree investigation. This method uses the multispecies coalescent (MSC) model to compare different models of species delimitation (Yang & Rannala 2010; Rannala & Yang 2013) and species phylogeny (Yang & Rannala 2014; Rannala & Yang 2017) in a Bayesian framework, accounting for incomplete lineage sorting due to ancestral polymorphism and gene tree-species tree discordance as implemented in analysis type A11. As our data consisted of only two loci but a large number of tentative species (*c.* 40–45) with few sequences per species, we encountered severe mixing and convergence problems in the MCMC runs in our analyses. Despite several attempts to adjust our priors and MCMC fine-tune values, we were unable to resolve these issues. Additional loci and/or more sequences per species might lead to better mixing and convergence (Yang & Rannala 2014). Carstens *et al.* (2013) recommend testing several different

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species delimitation programs and trust only those delimitations that are congruent across methods.

In mPTP, speciation is modelled by using the number of substitutions, that is branch lengths are compared between and among tentative species (Zhang *et al.* 2013). This means that long branches usually indicate the presence of a separate species. In several cases, mPTP split off one or two accessions of a morphospecies as a separately delimited species, usually placed on a longer branch and collected from a different continent than the remainder of the accessions (Figs 2 & 3). In *P. breviuscula*, our accessions from South-East Asia (i.e. New Caledonia, Philippines and Sri Lanka) were resolved as one species, while the accessions from La Réunion and Brazil were each delimited as a separate species (Figs 2 & 3). Also, in *P. cuyabensis* the Asian accession was delimited as a separate species from the South American accessions (Figs 2 & 3). In *P. isidiosa*, the case is slightly different: accessions from North America were separated from those from South America and Asia/Australia only in the ITS tree (Fig. 3). In other cases, mPTP split almost all accessions belonging to one morphospecies into different species, as for instance in *P. kalbii* (Figs 2 & 3). The species is pantropical and seemingly genetically highly variable. For the time being, we consider that the accessions belong to only one species in the instances mentioned above, because of the shared morphological characters and lack of lichen substances (or traces of atranorin). Hence, we recommend treating species delimitations inferred by statistical programs, such as mPTP, with caution.

In general, uneven sampling of a species is known to decrease mPTP accuracy (Zhang *et al.* 2013; Kapli *et al.* 2017). In our data, sampling additional specimens to improve the geographical coverage might adjust the delimitation results. On the other hand, mPTP results may be correct in recognizing populations on different continents as separate species if the extent of intercontinental genetic exchange has been severely restricted for a long time. Where there is no morphology or chemistry to support separate species, we have conservatively chosen to treat them as a single species.

Taxonomic conclusions

New species

In this study, we found several clades that seem to represent undescribed species. Based on our phylogenetic trees, we resurrect *P. melanoglauca* for chemotype 3 of *P. buettneri* and describe five new species: *P. amazonica* ('*Phyllopsora* sp.1'; Fig. 5A), *P. concinna* ('*P. parvifoliella* 2'; Fig. 5B), *P. furfurella* ('*P. furfuracea* 2'; Fig. 5C), *P. isidiosa* ('*P. byssiseda* 2'; Fig. 6A) and *P. neotinica* ('*P. chodatinica* 2'; Fig. 6B). Before describing the new species, we considered the possibility that they could belong to poorly understood or currently synonymized species. Based on the characteristic morphology and/or chemistry of the new species, however, we could not find any congruent specimens among the old types ('*P. furfuracea* 2' is excluded from that statement but see discussion below). Hence, we describe them here as new species.

The sequences of the newly described species grouped into distinct, strongly supported clades, indicating that they comprise entities to be recognized at species level (Figs 2 & 3). While we considered *P. amazonica* (Fig. 5A) to be a new species from first sight, the other four species were discovered only after phylogenetic analyses. These four species are morphologically and/or chemically similar or identical to well-known *Phyllopsora* species. *Phyllopsora neotinica* (Fig. 6B), for example, was at first regarded as a chemical strain of *P. chodatinica* due to its morphological similarity, although it lacks the name-giving xanthone chodatin. *Phyllopsora neotinica* occurs in the Neotropics only, while *P. chodatinica* occurs in the Palaeotropics. In *P. concinna* (Fig. 5B), we encountered a mixture of the morphology of *P. cinchonarum* and the chemistry of *P. parvifoliella*. Thus, specimens of *P. concinna* may be distinguished from each of the two aforementioned species by chemistry and morphology, respectively. Also *P. furfurella* (Fig. 5C) was initially assumed to belong to *P. furfuracea* because of the presence of furfuraceic acid. The

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former differs, however, in forming a white prothallus and only small and sparse isidia. Most of our *P. furfuracea* accessions (in addition to further unpublished sequences) clustered into a clade sister to *P. dolichospora* and *P. foliatella* (Figs 2 & 3, group A) and are morphologically closer to the type of *P. furfuracea* than the *P. furfurella* specimens. The type of *P. furfuracea* is old and was described from the Mariana Islands and, unfortunately, we could not obtain any fresh specimens from Micronesia or South-East Asia for sequencing. Some of the specimens of *P. isidiosa* (Fig. 6A) initially showed some similarity to *P. byssiseda*, while others rather resembled *P. isidiotyla*. Specimens of *P. isidiosa* form more delicate isidia than those found in *P. byssiseda* but are coarser than those in *P. isidiotyla*. Hence, *P. isidiosa* seems to be morphologically intermediate between these two species and single specimens of all three species may be challenging to correctly identify without DNA sequence data.

Three unidentified specimens (i.e. extract numbers 1017, 7227 and 7230), that are typically sterile and not containing lichen substances, resolved on long branches in close phylogenetic proximity to *P. canoumbrina*, *P. isidiotyla* and *P. malcolmii* (Figs 2–4). The identification of the specimens of *P. canoumbrina* and *P. isidiotyla*, however, is based only on morphological comparisons to the type material and is ambiguous as these two species are rather poorly understood and rarely collected. We regard the three unidentified specimens as morphologically different from their identified sister species. However, it is possible that some of them are conspecific with one or more of the species that we could not investigate molecularly and are generally poorly understood, for example *P. minor*. As all of the specimens show considerable sequence variation as well as minor morphological differences, it is possible that they represent one or more new species. However, we consider it premature to describe them now as we do not know the full extent of morphological, chemical and molecular variation in these groups. As the unidentified specimens seem to be closely related to group A (Figs 2–4), which contains many morphologically similar species, it is uncertain whether the minor morphological differences are diagnostic characters. Chemistry is also variable inside group A (Figs 2–4) since specimens of *P. foliatella* and *P. furfuracea* may also be acid deficient. Therefore, additional collections and/or more sequence data should be studied before new species are described.

Species not sequenced

In this study we accept 54 *Phyllopsora* species (including four new and one resurrected species) which we consider well understood (Taxonomy, part A). We generated sequences from 51 of the species listed in part A, but could not obtain sequences from *P. himalayensis*, *P. methoxymicareica* and *P. microdactyla* due to lack of fresh material. We still consider those to be well delimited by morphology and/or chemistry.

In addition, we have listed 19 species names which we consider poorly understood or doubtful, as well as fossil species (Taxonomy, part B). None of these could be sequenced. Many of the species are known only from collections made more than 30 years ago, rendering PCR amplification and Sanger sequencing of their DNA extracts a challenging task with a high risk of failure. In addition, many specimens are small and in poor condition so that destructive sampling for DNA sequencing is only acceptable when positive results are highly likely. So far, however, no such methods have been developed to routinely and successfully sequence old lichen material.

Kistenich *et al.* (2018*a*) excluded from the genus all studied species formerly assigned to *Phyllopsora* producing long, acicular ascospores and/or soredia. By extension, those characters provide a basis for suggesting that some of the species listed in part B may have to be excluded from *Phyllopsora*, such as *P. microphyllina* and *P. catervisorediata*. The former species forms acicular ascospores (Timdal 2011), while the latter forms soredia (Mishra *et al.* 2011). Mishra *et al.* (2011) suggest a close relationship between *P. catervisorediata* and *P. soralifera*; the latter is a species we find not to belong in *Phyllopsora* based on unpublished sequence data (see section

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on excluded species below and Taxonomy, part B). However, molecular data are needed before conclusions on species boundaries and generic affiliations are drawn for *P. catervisorediata* and *P. microphyllina*.

There are several species names in the genus *Phyllopsora* which are based solely on old and often poor quality types, for example *P. griseocastanea*, *P. manipurensis* and *P. subhyalina*. Thus, morphological characters of those specimens are difficult to interpret. Considering the high range of morphological (and chemical) variation exhibited in some species, it is currently impossible to ascertain whether some of our unidentified sequences belong to those species. It is also likely that additional 19th century names exist in *Phyllopsora*, originally described in the genera *Bacidia* or *Lecidea*, which we did not study.

Excluded species

Kistenich *et al.* (2018*a*) found the genus *Phyllopsora* to be polyphyletic. In addition to *Phyllopsora* s. str. in the *Ramalinaceae*, two species groups occurred in other clades of the same family, whereas *P. atrocarpa*, *P. lividocarpa* and *P. nigrocincta* belonged in the family *Malmideaceae*. Among the sequenced *Phyllopsora* specimens that did not belong to *Phyllopsora* s. str., three species grouped into the *Bacidia* clade: *P. sorediata* belongs in *Bacidia*, while *P. pertexta* and *P. borbonica* represent the resurrected genus *Sporacestra*. Based on a local BLAST search of unpublished sequences produced in the present study, we propose to exclude an additional seven species from *Phyllopsora*: *P. conwayensis*, *P. cognata*, *P. glaucescens*, *P. longispora*, *P. pocsii*, *P. soralifera* and *P. tobagensis*. To determine the respective generic placements of these species prior to making formal recombinations, detailed phylogenetic studies are necessary, including more representatives of each species and a broader taxonomic and distributional sampling of their close relatives. See also the Taxonomy section, part C, for a brief discussion of these species. *Phyllopsora pyrrhomelaena* is excluded from the genus *Phyllopsora* even though we were not able to produce sequences. This species appears to be a close relative of *P. atrocarpa*, *P. lividocarpa* and *P. nigrocincta* because of their shared apothecial anatomy, pigmentation, and chemistry (Timdal 2008, 2011). Hence, it is considered better accommodated in another genus in the *Malmideaceae*.

Our sequences of the isotype of *P. conwayensis* were found to be associated with the *Bacidia* clade. Both *P. conwayensis* and *P. sorediata* produce acicular ascospores, *c.* 25–30 × 0·8–1·2 µm in size, and have similar apothecial and thallus morphologies (see Elix 2006*c*; Aptroot *et al.* 2007), but *P. conwayensis* differs from *P. sorediata* in lacking soralia and having a more complex chemistry (Elix 2006*c*; Aptroot *et al.* 2007). Despite these differences, we do not discount the possibility that *P. conwayensis* might merely be a chemical strain of *P. sorediata*. However, before making formal combinations, further molecular studies including additional specimens of these two species are needed to clarify their status.

Four *Phyllopsora* species (i.e. *P. brakoae*, *P. lacerata*, *P. labriformis* and *P. leucophyllina*) occur in the *Toninia*-clade in Kistenich *et al.* (2018*a*). While *P. lacerata* was transferred to *Bacidina*, the new genus *Parallopsora* was described to accommodate the other three species. In the present study we also found unpublished sequences of *P. cognata*, *P. glaucescens*, *P. longispora*, *P. pocsii*, *P. soralifera* and *P. tobagensis* to group into this clade (data not shown). All species contain acicular ascospores (Swinscow & Krog 1985; Vězda 2003; Timdal 2008, 2011), indicating that they do not belong to *Phyllopsora* (Kistenich *et al.* 2018*a*). Our unpublished accessions of *P. longispora* clustered together with *Aciculopsora salmonea* Aptroot & Trest, the type of a recently described genus containing two species (Aptroot *et al.* 2006; Cáceres 2007). *Aciculopsora salmonea* differs from *P. longispora* in having a typical salmon-coloured hymenium, 7–9-septate ascospores and lacking both lichen substances and isidia (Swinscow & Krog 1985; Aptroot *et al.* 2006). In addition, *A. salmonea* is known from dry forests, while *P. longispora* prefers humid moist forests which are also typical habitats of species of *Phyllopsora* (Swinscow & Krog 1985; Aptroot

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et al. 2006). Further morphological and molecular studies are currently being prepared to investigate whether these two species are conspecific or represent different species in the same genus (S. Kistenich, G. Weerakoon & E. Timdal, unpublished data). The remaining *Phyllopsora* species share common features with each other and the three *Parallopsora* species, such as ascospore size and chemistry, but are variable in thallus morphology. We suggest transferring them to the new genus *Parallopsora* pending further molecular investigations.

Outlook

In this study, we have attempted to construct an initial baseline taxonomy of the tropical genus *Phyllopsora* by integrating phenotypic and genetic information to better understand species circumscriptions. Much remains to be done, however, to understand species delimitation in the genus. As PCR amplification and subsequent Sanger sequencing of many samples with some highly degraded DNA have proved to be challenging and time-consuming, the applicability of high throughput sequencing (HTS) platforms should be explored, for example using genome-skimming approaches. Thus, time and costs could be substantially reduced while gaining multiple phylogenetically relevant markers of many specimens simultaneously. Since the DNA of tropical *Phyllopsora* species seems to degrade rapidly after only a few years of storage, type material can rarely be sequenced. Here, HTS approaches might also be ideal for retrieving sequence data from such highly fragmented DNA, including old types (Prosser *et al.* 2016).

Phyllopsora is still poorly known in many parts of the world, such as the inner part of the Amazon, West and Central Africa, and South-East Asia. Generally, old-growth forests in tropical regions are becoming rare due to increased deforestation worldwide and are usually difficult to access. Obtaining formal sampling and export permissions poses an additional challenge. We discovered several new species from South America by exploring easily accessible secondary rainforests. However, little is known about the diversity of *Phyllopsora* in primeval tropical forests. As some *Phyllopsora* species are rarely collected or known from old type material only, more collections of *Phyllopsora* are needed to fully explore the diversity of the genus and the geographical distribution of the species.

Taxonomy

Some of the type specimens cited as 'holotype' by Swinscow & Krog (1981) and Brako (1991) are merely part of a gathering of a given species. In these cases, we have corrected the authors' use of 'holotype' to 'lectotype designated by' (Art. 9.10; see also McNeill 2014). In some cases, it is unclear whether the author(s) saw one or more specimens of the same gathering or perhaps even multiple gatherings. In these cases, we have kept the assignments favoured by those authors but note that some types of names listed by them as holotypes might be lectotypes.

The Taxonomy section is divided into three parts: part A comprises the well-understood, extant species as accepted in this study; part B contains those species, which are poorly understood or doubtful, as well as the two fossil species; part C lists excluded species. As species identification in *Phyllopsora* is difficult, we recommend consulting the morphological characteristics in Table S2 (see Supplementary Material, available online) in combination with chemistry in Table 2 for a first identification, and subsequently referring to the original species description. The *Phyllopsora* website can also be visited for additional pictures and information about the species: http://nhm2.uio.no/lichens/Phyllopsora.

A. Accepted, extant species

Phyllopsora africana Timdal & Krog

Mycotaxon **77:** 64 (2001); type: La Réunion, along road to Plaine d'Affouches, above Bras Citron, at point where road meets track, 20°57′S, 55°25′E, alt. 1220 m, 26-09-1996, *H. Krog & E. Timdal* RE8/13 (O L-798!—

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holotype; UPS!—isotype) (TLC: chlorophyllopsorin (major), argopsin (minor); DNA: MK352138 (mtSSU), MK352317 (ITS)).

Description. Timdal & Krog (2001), Elix (2009).

Chemistry. Chemotype 1: chlorophyllopsorin (major), argopsin (minor to trace); chemotype 2: methyl 2,7-dichloropsoromate (major), methyl 2,7-dichloronorpsoromate (submajor); chemotype 3: chlorophyllopsorin (major), methyl 2,7-dichloropsoromate (submajor), methyl 2,7-dichloronorpsoromate (submajor to trace), argopsin (minor to trace).

Distribution. Africa, Asia, Australia.

Discussion. Phyllopsora africana shows large morphological and chemical diversity. Some specimens (e.g. the holotype (509), 477, 1436 and 4037) form well-developed, cylindrical isidia, while others (e.g. 6348) form lacinules. The latter morphotype is reported here for the first time and observed in both chemotypes 1 and 3. The isidiate morphotype of *P. africana* is apparently morphologically identical to *P. ochroxantha* and *P. swinscowii*. Chemotype 1 represents the chemistry of the holotype; chemotype 2 is identical to the chemistry found in *P. swinscowii*; chemotype 3 represents a mixture of chemotypes 1 and 2. Our specimen of chemotype 2 (477) was initially identified as *P. swinscowii* due to its identical chemistry and morphology, but its sequences associate with those of *P. africana*. We have further sequences of *P. africana* chemotype 2 from Asia (Kistenich *et al.* 2019*a*) which confirm its nested position among the other *P. africana* chemotypes.

The five specimens of *P. africana* form a supported clade in our phylogenies (Figs 2 & 3). Most branches are long in the ITS tree and the mPTP analysis suggests splitting them into four species (Fig. 3), while the mtSSU tree resolves them as belonging to one species together with *P. swinscowii* (Fig. 2). *Phyllopsora africana* is sister to *P. swinscowii* in our phylogeny and is also closely related to *P. ochroxantha* (Figs 2–4, group C).

Phyllopsora africana and *P. swinscowii* overlap in their distribution range and are morphologically similar. They also overlap in their chemistry and our phylogenetic trees confirm that the two species are more closely related to each other than either is to *P. ochroxantha*. The current taxonomy seems unsatisfactory but it is questionable if all specimens assigned to *P. africana* comprise just one, highly variable species or a complex of species. As we cannot distinguish chemotype 2 of *P. africana* from *P. swinscowii* by either morphology or chemistry, they currently have to be considered a cryptic taxon pair. See Discussion for further comments.

Phyllopsora amazonica Kistenich & Timdal sp. nov.

MycoBank No.: MB 829272

Differs from *P. halei* in forming an irregular, effuse thallus with smaller areoles on a thin, white prothallus and in having more persistently marginate and less convex apothecia.

Type: Brazil, Pará, Melgaço, Floresta Nacional de Caxiuanã, Estação Científica Ferreira Penna, at the research station, 1°44·22′S, 51°27·32′W, 30 m alt., on tree trunk in tropical rainforest, 0·7 m above ground, trunk diam. 50 cm, 13 March 2015, *S. Kistenich & E. Timdal* 85 (MPEG!—holotype; O L-201094!—isotype) (TLC: atranorin and a series of terpenoids; DNA: MK352208 (mtSSU), MK352379 (ITS)).

(Fig. 5A)

Thallus effuse, crustose; *areoles* small, up to 0·4 diam., adnate, isodiametric, scattered when young, later often contiguous, plane to weakly convex, pale green to white, glabrous, not pubescent along the margin; *isidia* common, cylindrical to lageniform, simple, medium thick, up to 0·12 × 0·70 mm; *upper cortex* of type 1, 10–20 µm thick, containing crystals dissolving in K; *medulla* containing scattered crystals dissolving in K; *prothallus* thin, white.

Apothecia common, up to 1·0 mm diam., rounded, simple, plane to weakly convex, medium brown to dark brown, with a rather thick, dark brown to black, glabrous margin which may become more or less excluded when old; *excipulum* dark olivaceous brown in inner part, paler at the rim, containing some crystals dissolving in K (K–); *hypothecium* dark olivaceous brown, not containing crystals; *epithecium* colourless, K–; *ascospores*

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narrowly ellipsoid, simple, 7–10 × 2–3 µm (n = 20, from the holotype).

Conidiomata not seen.

Chemistry. Atranorin (major) and a series of terpenoids, the main one in R_f classes A: 6–7, B′: 8, C: 6–7 (chemistry identical to that of *P. halei* chemotype 1).

Etymology. The species is described from the Amazonian rainforest.

Distribution. Brazil (Pará).

Discussion. The species is resolved as a separate species in the mPTP analyses (Figs 2 & 3). It is sister to *P. halei* (Figs 3 & 4) and *P. pyxinoides* (Fig. 4). The species resembles *P. halei* in forming adnate areoles with thick, partly lageniform isidia and it contains the same lichen substances as *P. halei* chemotype 1. It differs, however, in forming a less prominent, thinner, white (not reddish brown) prothallus and in having isidia growing sometimes directly out of the prothallus. While *P. halei* forms rosette-like thalli, *P. amazonica* produces irregular, effuse thalli. In addition, the apothecia of *P. amazonica* are more persistently marginate and less convex than those in *P. halei*.

Additional specimen examined. **Brazil:** *Pará*: Paragominas, Hydro mining area, collecting site 2, 3°14·82′S, 47°40·99′W, 150 m alt., on tree trunk in tropical rainforest, in the canopy of a felled tree, 2014, *R. S. Barbosa, R. Haugan & E. Timdal* 90 (MPEG, O L-193960) [DNA: MK352194 (mtSSU), MK352365 (ITS)].

Phyllopsora breviuscula (Nyl.) Müll. Arg.

Bull. Herb. Boissier **2**(App. 1)**:** 45 (1894).—*Lecidea breviuscula* Nyl., *Ann. Sci. Nat., Bot., Sér. 4* **19:** 339 (1863); type: Cuba, s. loc., *C. Wright* (H-NYL 20557!—lectotype, designated by Swinscow & Krog (1981): 225; B 60-35829!, UPS L-74707!—probably isolectotypes, issued as Tuckerman, *Wright Lich. Cub.* No. 181, more isolectotypes listed by Brako (1991): 56) (TLC: no lichen substances).

Lecidea subbreviuscula Nyl., *Sert. Lich. Trop.*: 40 (1891).—*Phyllopsora subbreviuscula* (Nyl.) Zahlbr., *Cat. Lich. Univ.* **4**(3)**:** 401 (1926); type: Cuba, s. loc., *C. Wright* (H-NYL 20524!—holotype; FH-TUCK 2922, isotype, not seen, issued as Tuckerman, *Wright Lich. Cub.*, ser. 2, No. 120).

Phyllopsora brachyspora Müll. Arg., *Bot. Jahrb. Syst.* **20:** 264 (1895); type: Tanzania, Usambara, Hochwald ob Kwa Mstufa, *Holst* 9181 pr. p. (G 00066323, upper right specimen—lectotype, designated here, MycoBank typification MBT 387683, image seen; M 0024443—isolectotype, image seen; BM, W—isolectotypes, not seen) (TLC (Swinscow & Krog 1981): no lichen substances. Synonymy according to Swinscow & Krog (1981) and Brako (1991)).

Descriptions. Timdal & Krog (2001), Elix (2009).

Chemistry. No lichen substances.

Distribution. Pantropical.

Discussion. All accessions (four in the mtSSU and five in the ITS tree) form a well-supported clade sister to *P. mauritiana* in our phylogenies (Figs 2–4). The mPTP delimitation analyses in both trees split the accessions into three and four entities, respectively (Figs 2 & 3). Our first impression when studying the Asian specimens (Fig. 1) morphologically was that they represented an unknown species. These specimens exhibit strongly ascending squamules that are both narrower and longer than those known from neotropical *P. breviuscula*, which has more adnate and procumbent squamules. When comparing all five specimens, we found that the specimen from La Réunion showed a transient morphology between the two extremes in forming medium-long but adnate squamules. We therefore consider these accessions to belong to the same species, *P. breviuscula*, developing different morphologies depending on the geographical region.

Phyllopsora buettneri (Müll. Arg.) Zahlbr.

Cat. Lich. Univ. **4**(3)**:** 396 (1926).—*Psora buettneri* Müll. Arg., *Bot. Jahrb. Syst.* **15:** 506 (1893); type: Togo, Bismarksburg, *Büttner* L. Afr. 7 (G 00066290—holotype, image seen; BM!—isotype) (TLC (Swinscow & Krog 1981): pannarin, zeorin, fatty acids).

Lecidea munda Malme, *Ark. Bot.* **28A**(7)**:** 49 (1936).—*Phyllopsora munda* (Malme) Zahlbr., *Cat. Lich. Univ.* **10** (24)**:** 377 (1939); type: Brazil, Rio Grande do Sul, Hamburgerberg pr. São Leopold, 18-10-1892, *G. A. Malme* Lich. Regnell. 617B (S!—holotype) (TLC (Brako 1991): pannarin, phyllopsorin, zeorin).

Lecidea schizophylloides Malme, *Ark. Bot.* **28A**(7)**:** 45 (1936); type: Brazil, Rio Grande do Sul, Silveira Martins, 07-03-1893, *G. A. Malme* Lich. Regnell. 1227B [sic!, in protologue: '1251B'] (S!—holotype) (TLC (Brako 1991): pannarin, phyllopsorin, zeorin).

Descriptions. Swinscow & Krog (1981), Timdal & Krog (2001), Timdal (2008, as *P. buettneri* chemotypes 1 and 2), Elix (2009).

Chemistry. Chemotype 1: pannarin, zeorin; chemotype 2: pannarin, phyllopsorin, zeorin; chemotype 3: dechloropannarin, zeorin. An additional chemotype (4) is reported from Norfolk Island (Elix 2006*b*), containing argopsin, norargopsin and zeorin. According to Elix (2009), chemotypes containing pannarin as a major compound may also contain dechloropannarin as minor or trace compound, and vice versa.

Distribution. Chemotype 1: Africa, Asia; chemotype 2: Central and South America; chemotype 3: Asia; chemotype 4: Australia.

Discussion. The chemotypes of *P. buettneri* were discussed by Brako (1991) and Timdal (2008, 2011). The chemotype containing vicanicin, norvicanicin and zeorin (referred to as chemotype 3 in Timdal (2011)) is accepted here as a distinct species, *P. melanoglauca*, falling outside group B (Figs 2 & 3). Hence, *P. buettneri* now consists of three chemotypes (chemotype 1 from Africa and Asia, chemotype 2 from Central and South America, and chemotype 3 from Asia), all containing pannarin and/or dechloropannarin, with a possible fourth Australasian chemotype (argopsin; see also discussion for *P. subhispidula*). However, we were not able to examine the last chemotype. The accessions of chemotypes 1, 2 and 3 group into a well-supported clade (Figs 3 & 4). In the ITS tree, mPTP splits all chemotypes into separate species (Fig. 3), whereas the mPTP analysis on the mtSSU tree delimits one species for all accessions (Fig. 2). All chemotypes are apparently morphologically identical and group together in the ITS and *BEAST trees (Figs 3 & 4); thus, we assume they belong to the same species. *Phyllopsora buettneri* is morphologically rather similar to *P. chodatinica* and *P. porphyromelaena*. These species differ mainly in their chemistries and exhibit slightly different spore sizes, squamule forms and presence of pruina. See Discussion for more detail on this species complex.

Phyllopsora byssiseda (Nyl.) Zahlbr.

Cat. Lich. Univ. **4**(3)**:** 396 (1926).—*Lecidea byssiseda* Nyl. in Hue, *Nouv. Arch. Mus. Hist. Nat., Sér. 3* **3:** 103 (1891); type: Mexico, s. loc., *Fr. Müller* s. n. (H-NYL 20517!—holotype) (TLC: no lichen substances).

Description. Timdal (2011).

Chemistry. No lichen substances or atranorin (minor to trace).

Distribution. Central and South America.

Discussion. In this study, we originally included eight specimens believed to represent *P. byssiseda*. However, they resolved into two separate clades (Figs 2 & 3) and six of the specimens correspond to the new species *P. isidiosa* (Fig. 6A).

Our two remaining accessions of *P. byssiseda* form a strongly supported clade sister to *P. fendleri* in the phylogenetic trees (Figs 2–4). mPTP resolves them as a distinct species in both analyses (Figs 2 & 3). *Phyllopsora byssiseda* is morphologically similar to its sister species in forming a dense white prothallus with large, lobate squamules with a pubescent margin. While *P. fendleri* tends to be richly fertile, *P. byssiseda* forms numerous isidia. The two species have also been reported to differ slightly in chemistry, *P. fendleri* being acid deficient (Brako 1991) and *P. byssiseda* containing traces of atranorin (Timdal 2011). In our sequenced specimens of *P. byssiseda*, we found one (4739) without lichen substances, while the other (4737) contained not only atranorin but also two additional unknown compounds (possibly contaminants). The two sequenced specimens of *P. fendleri* contained atranorin (2098) or no lichen substances (7473). Apothecia were found in one of the *P. byssiseda* specimens and a few, small isidia in the richly fertile *P. fendleri* specimens. Based on these discoveries, the morphological and chemical differences between the two species become small. Even though they are resolved as two distinct species in both analyses, we find a similar variation of branch lengths in other species, for example in *P. kalbii*, and regard it as not unlikely that they belong to the same species despite the mPTP results.

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Phyllopsora canoumbrina (Vain.) Brako

Mycotaxon **35:** 12 (1989).—*Lecidea canoumbrina* Vain., *Proc. Amer. Acad. Arts. Sci.* **58:** 135 (1923); type: Trinidad and Tobago, Trinidad, Maraval Valley, ad corticem arboris, *R. Thaxter* 19 (FH—lectotype, designated by Brako (1991): 33 (as 'holotype', Art. 9.10), not seen; TUR-V 23680!—isolectotype) (TLC: no lichen substances).

Lecidea granulifera Fink in Hedrick, *Mycologia* **22:** 252 (1930); type: Puerto Rico, Rio de Maricao, on rock, 14-02-1915, *N. L. Britton & J. F. Cowell* 4235 (MICH—holotype, not seen; NY!—isotype).

Description. Brako (1991).

Chemistry. No lichen substances.

Distribution. Central and South America.

Discussion. We know of no reliably identified and recently collected material from the geographical region from which this poorly understood species was described (the West Indies). The isotype is in a poor condition and was not used for DNA extraction. The sequenced specimen is from Brazil and identified as *P. canoumbrina* as it is richly fertile, has an almost crustose thallus on a white prothallus, forms minute squamules, small cylindrical isidia, lacks lichen substances, and the ascospores (5·0–7·5 × 2–3 µm) are largely congruent with those measured from the isotype (6·5–9·5 × 2·5–3·0 µm; Brako 1991). Our accession of *P. canoumbrina* is supported as sister to *P. isidiotyla* (Figs 2–4) but sits on a long branch (Figs 2 & 3) and is morphologically clearly distinct from that species. The mPTP analyses resolve the accession as a separate entity (Figs 2 & 3).

Phyllopsora castaneocincta (Hue) Kistenich & Timdal comb. nov.

MycoBank No.: MB 82927

Pannaria castaneocincta Hue, *Nouv. Arch. Mus. Hist. Nat., Sér. 4* **8:** 262 (1906); type: Japan, Kin. Kuwasan, 1902, s. coll. 5183 (PC 0012756!—holotype) (TLC: furfuraceic acid).

Lecidea kiiensis Vain., *Bot. Mag. (Tokyo)* **35:** 67 (1921).—*Phyllopsora kiiensis* (Vain.) Elix, *Fl. Australia* **57:** 52 (2009); type: Japan, Prov. Kii, 30-12-1918, *Yasuda* 268 (TUR-V 22631—holotype, not seen; TNS!—isotype) (TLC: furfuraceic acid).

Phyllopsora phaeoglauca (Vain.) Zahlbr., *Cat. Lich. Univ.* **4**(3)**:** 400 (1926).—*Lecidea phaeoglauca* Vain., *Ann. Acad. Sci. Fenn., Ser. A* **15**(6)**:** 112 (1921); type: Philippines, Luzon, Prov. Bataan, Limay, 31-12-1909, *C. B. Robinson* 9631 (TUR-V 22617!—lectotype, designated by Swinscow & Krog (1981): 244) (TLC: no lichen substances).

Description. Timdal & Krog (2001) and Elix (2009), both as *P. kiiensis*.

Chemistry. Furfuraceic acid (major) or rarely no lichen substances.

Distribution. Africa, Asia, Australia.

Discussion. The name *Phyllopsora kiiensis* is antedated by *P. castaneocincta* and has been mistakenly used for this species so far. *Phyllopsora phaeoglauca* is also synonymized here as its lectotype apparently represents the acid-deficient chemotype of *P. castaneocincta*, which Kistenich *et al.* (2019*a*) show is nested within furfuraceic acid-containing specimens of that species. The five accessions of *P. castaneocincta* in this paper all contain furfuraceic acid and group together in a strongly supported clade, where the African specimens form a group distinct from the Asian and Australian ones (Figs 2 & 3). All specimens are resolved as one species in the mtSSU tree (Fig. 2), while the mPTP analysis of the ITS tree separates them into three entities according to continent (Fig. 3). We still consider them to belong to the same species as they all share a characteristic morphology with a thick brownish prothallus, adnate squamules and cylindrical isidia, as well as the presence of furfuraceic acid. *Phyllopsora castaneocincta* is weakly resolved as sister to *P. mediocris* and *P. parvifolia* in the mtSSU tree (Fig. 2), whereas it is found in a strongly supported clade with *P. confusa*, *P. foliata*, *P. loekoesii*, *P. mediocris*, *P. neofoliata* and *P. parvifolia* in the ITS and the *BEAST trees (Figs 3 & 4). It is distinguished from phylogenetically related species by morphology and chemistry.

Phyllopsora chlorophaea (Müll. Arg.) Müll. Arg.

Bull. Soc. Roy. Bot. Belgique **32:** 132 (1893 [1894?]).—*Psora chlorophaea* Müll. Arg., *Flora* **70:** 320 (1887); type: Brazil, São Paulo, Apiahy, 06-1881, *Puiggari* 1721 (G 00293365—lectotype, designated by Swinscow & Krog (1981): 228, image seen) (TLC (Swinscow & Krog 1981): no lichen substances).

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Lecidea haemophaea var. *subparvifolia* Müll. Arg., *Flora* **60:** 473 (1877).—*Phyllopsora subparvifolia* (Müll. Arg.) Müll. Arg., *Hedwigia* **34:** 141 (1895); type: Venezuela, Caracas, *Ernst* 114 (G 00293364—holotype, image seen) (TLC (Swinscow & Krog 1981): no lichen substances). Synonymy according to Swinscow & Krog (1981) and Brako (1991).

Lecidea furfuracea f. *schizophylla* Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2)**:** 47 (1890).—*Lecidea schizophylla* (Vain.) Malme, *Ark. Bot.* **28A**(7)**:** 43 (1936).—*Phyllopsora schizophylla* (Vain.) Gotth. Schneid., *Biblioth. Lichenol.* **13:** 172 (1980), nom. inval., Art. 36.1 (a); type: Brazil, Minas Lafayette, *E. A. Vainio* (TUR-V 22641—lectotype, designated by Swinscow & Krog (1981): 228, not seen) (TLC (Swinscow & Krog 1981): triterpenoid, trace). Synonymy according to Swinscow & Krog (1981) and Brako (1991).

Descriptions. Timdal & Krog (2001), Timdal (2008).

Chemistry. Chemotype 1: no lichen substances or atranorin (trace to minor); chemotype 2: furfuraceic acid and sometimes atranorin (trace).

Distribution. Central and South America, Africa.

Discussion. All accessions of *P. chlorophaea* group together in a supported clade in the phylogenetic trees (Figs 2 & 3, group B). They are resolved as one species in the ITS tree (Fig. 3), while mPTP suggested four delimited species in the mtSSU tree, which has long branches (Fig. 2). All specimens are recognized by the same morphological features: ascending, lacinulate squamules attached to a well-developed, reddish brown prothallus, dark brown apothecia and narrowly ellipsoid to fusiform ascospores. Hence, we assume they all belong to the same species. *Phyllopsora chlorophaea* is resolved in a clade together with the new species *P. neotinica* and the *buettneri-chodatinica-porphyromelaena* complex (Figs 2 & 4, group B), with which it shares the presence of lacinules. It is, however, readily distinguished from those species by forming smaller squamules and by containing either no lichen substances or furfuraceic acid, often with small amounts of atranorin.

Phyllopsora chodatinica Elix

Australas. Lichenol. **59:** 23 (2006); type: Australia, Queensland, Blencoe Creek, Cardwell Range, 48 km NW of Cardwell, 18°03′S, 145°39′E, 740 m alt., on mossy trunk in *Lauraceae-Syzygium-Prunus*-dominated forest, 17-06-1986, *J. Elix & H. Streimann* 20109 (BRI—holotype, not seen; CANB—isotype, not seen).

Descriptions. Elix (2006*c*, 2009).

Chemistry. A chemosyndrome of xanthones based on chodatin (Elix 2006*c*).

Distribution. Australasia and Oceania.

Discussion. We included seven specimens in the phylogenetic analyses, originally identified as *P. chodatinica* based on morphology and chemistry, as well as a paratype. The species splits into two different, strongly supported clades, one containing the palaeotropical specimens including the paratype, and the other comprising only neotropical specimens (Figs 2 & 3). The mPTP analyses delimits each clade as a separate species (Figs 2 & 3). The two clades are rather closely related to each other and are found as sister to *P. buettneri*, *P. chlorophaea* and *P. porphyromelaena* (Figs 2–4, group B). All species within group B are morphologically very similar but can be separated by their chemical compounds. We describe here the neotropical clade of *P. chodatinica* as the new species *P. neotinica* (Fig. 6B); see that species for further discussion. *Phyllopsora chodatinica* can be separated from *P. neotinica* by chemistry: both species contain various xanthones but chodatin is found only in *P. chodatinica*, while *P. neotinica* usually also contains argopsin and zeorin.

Phyllopsora cinchonarum (Fée) Timdal

Lichenologist **40:** 346 (2008).—*Triclinum cinchonarum* Fée, *Essai Crypt. Écorc.*: 148 (1825); type: Fée, *Essai Crypt. Écorc.*: Tab. 33, Fig. 4 (1825) (lectotype, designated by Jørgensen (2003): 76, with epitype: "the type specimen of *Physcidia endococcinea* Zahlbr. (W!)").—*Physcidia endococcinea* Zahlbr., *Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl.* **83:** 159 (1909).—*Squamacidia janeirensis* var. *endococcinea* (Zahlbr.) Brako, *Mycotaxon* **35:** 10 (1989); type: Brazil, São Paulo, prope Barra Mansa in districtu urbis Itapecirica, in silvaticis, *c.* 1000 m alt., 06-1901, *V. Schiffner* s. n. (W 8343!—holotype) (TLC: atranorin, lobaric acid, scarlet pigment in R_f classes 1–2:1:1).

Thalloidima janeirense Müll. Arg., *Hedwigia* **31:** 280 (1892).—*Phyllopsora janeirensis* (Müll. Arg.) Swinscow & Krog, *Lichenologist* **13:** 242 (1981).—*Squamacidia janeirensis* (Müll. Arg.) Brako, *Mycotaxon* **35:** 8 (1989); type: Brazil, Rio de Janeiro, s. loc., *Portella* s. n. (BM!—

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holotype; G 00294395—isotype, image seen) (TLC: fumarprotocetraric acid, lobaric acid).

Phyllopsora stenosperma Zahlbr., *Repert. Spec. Nov. Regni Veg.* **33:** 44 (1933); type: Taiwan, Chiayi Prov., Mt. Arisan, Toroyen, 24-12-1925, *Y. Asahina* F-170 (W—lectotype, designated by Swinscow & Krog (1981): 245 (as 'holotype', Art. 9.10), not seen; TNS!—isolectotype; NY—isolectotype, not seen) (TLC: atranorin, lobaric acid).

Descriptions. Brako (1989, as *Squamacidia janeirensis*), Timdal (2008) and Elix (2009, as *Triclinum cinchonarum*).

Chemistry. Lobaric acid (major) and often atranorin, fumarprotocetraric acid, an unknown substance, and/or a scarlet pigment. Additional compounds are reported by Aptroot *et al.* (2007) and Elix (2007).

Distribution. Central and South America, Asia, Australia.

Discussion. We included four accessions of *P. cinchonarum* in our study. All of them clustered together in a strongly supported clade in both phylogenetic trees (Figs 2 & 3) and are resolved as phylogenetic sister to *P. concinna* (Figs 2 & 4). The mPTP analysis of the mtSSU tree resolves *P. cinchonarum* as one species (Fig. 2), while the ITS mPTP analysis separates the two included accessions (Fig. 3). All four specimens agree in morphology and chemistry (lobaric acid in all, atranorin and fumarprotocetraric acid being variable) and we therefore assume they belong to one species. *Phyllopsora cinchonarum* is morphologically similar to its sister species *P. concinna* in forming long, simple isidia and adnate to ascending, medium-sized squamules on a white prothallus. It is readily distinguished, however, by its chemical composition as *P. concinna* contains parvifoliellin instead of lobaric acid.

The species was first described as *Triclinum cinchonarum* and is the type species of the genus *Triclinum* Fée. As the name *Triclinum* antedates *Phyllopsora*, we propose the latter for conservation (Kistenich *et al.* 2019*b*). Unfortunately, the specimens sequenced here lack the characteristic scarlet pigment present in the epitype but, based on general morphology and chemistry (lobaric acid), we believe that the presence of the pigment merely represents a minor chemical variation in some specimens within the species.

Phyllopsora concinna Kistenich & Timdal sp. nov.

MycoBank No.: MB 829273

Differs from the chemically similar species *P. parvifoliella* and *P. rappiana* in forming larger isidia, having a white prothallus, an apothecial margin paler than the disc, and longer and broader ascospores; differs from the morphologically similar species *P. cinchonarum* in containing parvifoliellin, not lobaric acid.

Type: Venezuela, Capital District, Parque Nacional Macarao, 1·5 km E of El Junquito, 10°27·60′N, 67° 04·45′W, 1920 m alt., on tree trunk by visitor's centre, 0·4–1·2 m above ground, trunk diam. 60 cm, 12 November 2015, *M. S. Dahl, J. E. Hernández M., S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-225 (O L-202505!—holotype; VEN!—isotype) (TLC: atranorin (major), parvifoliellin (major); DNA: MK352236 (mtSSU), MK352404 (ITS)).

(Fig. 5B)

Thallus effuse, squamulose; squamules medium sized, adnate, isodiametrical or rarely somewhat elongated at the thallus margin, entire to crenulate or incised, plane to weakly convex; upper side pale green, glabrous, epruinose; *margin* concolorous with upper side, sometimes finely pubescent; *isidia* numerous, both marginal and laminal on the squamules, cylindrical, simple, up to 0·2 × 1·5 mm; *upper cortex* of type 1, 35–60 µm thick, containing crystals dissolving in K (K–); *medulla* containing a few scattered crystals dissolving in K (K–); *prothallus* usually well developed, white.

Apothecia rare, up to 1 mm diam., irregular, conglomerate, weakly convex, medium brown, with an indistinct, paler margin; *ascospores* narrowly ellipsoid to fusiform, simple, 12·5–16·0 × 3·5–4·0 µm ($n = 20$).

Conidiomata not seen.

Chemistry. Atranorin (major), parvifoliellin (major).

Etymology. The epithet refers to the species being beautiful.

Distribution. Central and South America.

Discussion. The four accessions of this species used here were originally identified

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as *P. parvifoliella* on the basis that the specimens contained parvifoliellin. However, they are resolved in a separate, strongly supported clade (Figs 2 & 3), being clearly distinct from *P. parvifoliella* and sister to *P. cinchonarum* (Figs 2 & 4). Upon closer morphological investigation, we found the specimens to resemble *P. cinchonarum* more than *P. parvifoliella*. mPTP resolves the accessions of *P. concinna* as representing two species in the mtSSU tree (Fig. 2) and three in the ITS tree (Fig. 3). We anyway treat them as a single species based on morphology and chemistry, and attribute the mPTP results to regional variation among populations. The species is separated from the two other species that contain parvifoliellin (*P. parvifoliella* and *P. rappiana*) mainly by forming larger isidia, having a white prothallus and larger ascospores. It is distinguished from the morphologically very similar *P. cinchonarum* mainly by the presence of parvifoliellin rather than lobaric acid.

Additional specimens examined. **Brazil:** *Rio de Janeiro*: Parque Nacional do Itatiaia, surroundings of Lago Azul, 22°27·10′S, 44°36·92′W, 830 m alt., on tree trunk in Atlantic rainforest, 2015, *M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-359 (O L-202639); surroundings of Abrigo Lamego, 22° 25·66′S, 44°37·19′W, 1140 m alt., on tree trunk in Atlantic rainforest, 2015, *M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-405 (O L-202685); along trail to Três Picos, 22°26·04′S, 44°36·82′W, 1090 m alt., on *Arecaceae* trunk in Atlantic rainforest, 2015, *M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-445 (O L-202725) [DNA: MK352224 (mtSSU), MK352395 (ITS)].—**Ecuador:** *Pastaza*: Mera, 1100 m alt., roadside, epiphyte, 1972, *L. Arvidsson & D. Nilson* 206 (GB).—**Guatemala:** *Alta Verapaz*: Parque Nacional Las Victorias, Cobán (tierra templada), 1100–1300 m alt., *Pinus*-dominated forest, on *Liquidambar styraciflua*, 13 viii 2002, *C. Andersohn* s. n. (B! 60 127220) [DNA: MK352251 (mtSSU), MK352418 (ITS)].—**Panama:** *Coclé*: SW of Panama City, NW of small village El Valle, in old crater of extinct volcano, trail in tropical forest, from El Valle up to La India Dormida, 8°36·9′N, 80° 08·27′W, 585 m alt., edge forest/field, 2010, *P. van den Boom* 43947 (hb. v. d. Boom) [DNA: MK352202 (mtSSU), MK352373 (ITS)].

Phyllopsora confusa Swinscow & Krog

Lichenologist **13:** 229 (1981); type: Kenya, Central Province, Kirinyaga District, Mt. Kenya, 2 km NW of Irangi Forest Station in damp deciduous forest near River Ena, 0°20′S, 37°28′E, 2000 m alt., 02-1972, *H. Krog & T. D. V. Swinscow* K48/177 (O L-1145!—holotype) (TLC: no lichen substances; DNA: MK352140 (mtSSU), MK352318 (ITS)).

Descriptions. Swinscow & Krog (1981), Timdal & Krog (2001), Elix (2009).

Chemistry. No lichen substances.

Distribution. Pantropical.

Discussion. The seven accessions of *P. confusa*, including that from the holotype, group together in a strongly supported clade in both phylogenies (Figs 2 & 3). All specimens are resolved here as sister to *P. loekoesii* (Figs 2–4) from which they are distinguished by forming more distinct lacinules and shorter ascospores. In the species delimitation analyses, mPTP splits the accessions into two and four species in both trees (Figs 2 & 3), respectively. While the holotype groups together with three/four other specimens, the specimen from Ecuador and one from Venezuela are resolved as a different species in both mPTP analyses (Figs 2 & 3). It is interesting to note, however, that the two specimens from Venezuela end up in two different clades. These two specimens do not show any striking morphological or chemical differences to the other *P. confusa* specimens. Therefore, we assume that all specimens belong to the same species. To investigate whether the separated specimens form a different (cryptic) species or whether they merely reflect intraspecific genetic variation, more specimens of *P. confusa* should be collected and analyzed genetically.

The species is difficult to understand morphologically, having a thallus forming minute squamules that effectively turn into lacinules (fragmenting into diaspores). Swinscow & Krog (1981), in the protologue, were unsure about the extent of morphological variation present in this species. In our experience, identification of this species is often based on a process of elimination: when no significant morphological characteristics are present in a sterile, lacinulate specimen and TLC results are negative, we assume the specimen to be *P. confusa* until contradicted by DNA sequence data.

Phyllopsora corallina (Eschw.) Müll. Arg.

Bot. Jahrb. Syst. **20:** 264 (1895).—*Lecidea corallina* Eschw. in Martius, *Fl. Bras. Enum. Pl.* **1**(1)**:** 256 (1833); type: Brazil, Bahia, *Martius* s. n. (M 0024451—holotype, image seen; G 00293368, H-NYL 20483—isotypes, images seen) (TLC (Brako 1991): no lichen substances).

Descriptions. Timdal & Krog (2001), Elix (2009).

Chemistry. No lichen substances or small amounts of argopsin or atranorin.

Distribution. Neotropical; palaeotropical records need confirmation.

Discussion. The interpretation of *P. corallina* remains difficult. According to Brako (1991), the holotype does not contain lichen substances, although the species (as *P. corallina* var. *corallina*) may contain atranorin. In this study, we use four neotropical specimens which conform morphologically to our understanding of the species (i.e. to that of Timdal & Krog 2001), but some contain minor amounts or traces of what appears to be argopsin. The four specimens form a strongly supported clade and are resolved as a single species in the mPTP analyses (Figs 2 & 3). The palaeotropical species *P. martinii* is morphologically similar to *P. corallina* but differs in forming shorter ascospores and in containing argopsin, norargopsin and chlorophyllopsorin (see Timdal & Krog 2001). The other species in this clade can be distinguished from *P. corallina* mainly by forming more distinct morphological characters or different lichen substances.

Phyllopsora cuyabensis (Malme) Zahlbr.

Cat. Lich. Univ. **10**(24)**:** 377 (1939).—*Lecidea cuyabensis* Malme, *Ark. Bot.* **28A**(7)**:** 48 (1936); type: Brazil, Mato Grosso, Serra da Chapada, Buritis, in silva umbrosa, 26-06-1894, *G. O. A. Malme* s. n. (S!—lectotype, designated by Brako (1991): 44 (as 'holotype', Art. 9.10); UPS L-010377!—isolectotype) (TLC (Brako 1991): no lichen substances).

Description. Timdal (2008).

Chemistry. No lichen substances.

Distribution. Central and South America, Asia.

Discussion. The five accessions of *P. cuyabensis* group into a strongly supported clade in both phylogenetic trees (Figs 2 & 3). The specimen from Thailand is separated from the four neotropical specimens in both mPTP analyses (Figs 2 & 3). As all five specimens share the same morphology, we assume they represent the same species and the long branches result from the geographical distance between the populations. The species is weakly resolved as sister to *P. kalbii* (Figs 2 & 4) and forms a larger clade with *P. byssiseda* and *P. fendleri* (Figs 2 & 4). The species forms a thallus reminiscent of that of the former genus *Crocynia* (i.e. non-corticate and more or less rosette-forming), which readily distinguishes it from *P. kalbii*. However, it is not closely related to the two species of *Crocynia* in our phylogeny (*P. gossypina* and *P. pyxinoides*) (Figs 2 & 3). Hence, we assume that the reduction of the upper cortex has occurred independently in *P. cuyabensis* and the former species of *Crocynia*.

Phyllopsora dolichospora Timdal & Krog

Mycotaxon **77:** 76 (2001); type: Mauritius, Plaine Wilhems, Macchabee Forest, 0·5–1 km ESE of Macchabee kiosk, 20°24′S, 57°26′E, 600 m alt., 21-11-1991, *H. Krog & E. Timdal* MAU65/22 (O L-22197!—holotype) (TLC: furfuraceic acid, methyl furfuraceiate, methyl homofurfuraceiate; DNA: MK352141 (mtSSU), MK352319 (ITS)).

Description. Timdal & Krog (2001).

Chemistry. Furfuraceic acid (major), methyl furfuraceiate (major or minor) and methyl homofurfuraceiate (major or minor).

Distribution. Africa, Asia.

Discussion. All accessions of *P. dolichospora*, including the holotype, form a strongly supported clade in our phylogenetic analyses (Figs 2 & 3). They are resolved as one species in the mtSSU mPTP analysis (Fig. 2) but are divided into three species in the ITS mPTP analysis (Fig. 3), where the accessions appear on long branches. We also observed large introns in the residual 18S region, sequenced as part of the primer ITS-1F but trimmed for the phylogenetic analyses, that were not found in other *Phyllopsora* species. The specimens showed some morphological variation

regarding the quantity of isidia and colour of the prothallus corresponding to the different lineages in Fig. 2. We still consider them to belong to the same species as they all share the unique chemistry consisting of furfuraceic acid, methyl furfuraceiate and methyl homofurfuraceiate. The species groups into a weakly supported clade with *P. furfuracea* and *P. foliatella* (Figs 2–4). It resembles both species morphologically by forming an areolate thallus, which often only consists of the prothallus and long isidia. This makes it hard to distinguish between them based on morphology, and many of our specimens had been identified as *P. furfuracea* after an initial morphological investigation. *Phyllopsora dolichospora* is distinguished from the other species by its long ascospores and its distinct chemistry (Table 2).

Phyllopsora fendleri (Tuck. & Mont.) Müll. Arg.

Bot. Jahrb. Syst. **20:** 264 (1895).—*Biatora fendleri* Tuck. & Mont. in Montagne, *Ann. Sci. Nat., Bot., Sér. 4* **8:** 296 (1857); type: Venezuela, *Fendler* (FH-TUCK 2923—lectotype, designated by Brako (1991): 44 (as 'holotype', Art. 9.10), not seen; H-NYL 20523—isolectotype, image seen) (TLC (Brako 1991): no lichen substances).

Description. Brako (1991).

Chemistry. No lichen substances or atranorin (minor).

Distribution. Central and South America.

Discussion. Our two accessions of *P. fendleri* cluster together in a strongly supported clade as sister to *P. byssiseda* (Figs 2–4) and are resolved as one species in the mPTP analyses (Figs 2 & 3). *Phyllopsora fendleri* is morphologically almost identical to the isidiate *P. byssiseda* but differs in typically being richly fertile and forming no or few isidia. Both may contain (traces of) atranorin. It is possible that they are conspecific but the few available specimens of both species make evaluation of the morphological variation difficult. See also the discussion under *P. byssiseda*.

Phyllopsora foliata (Stirt.) Zahlbr.

Cat. Lich. Univ. **4**(3)**:** 397 (1926).—*Lecidea foliata* Stirt., *Trans. & Proc. Roy. Soc. Victoria* **17:** 71 (1881); type: Australia, Queensland, Brisbane, *F. M. Bailey* 156 (GLAM—lectotype, designated by Rogers (1982): 504, not seen; BRI—isolectotype, not seen).

Description. Elix (2009).

Chemistry. No lichen substances.

Distribution. Asia, Australia.

Discussion. Our three accessions of *P. foliata* group together in a strongly supported clade in the mtSSU tree (Fig. 2). However, only two accessions group together with strong support, without the Japanese accession, in the ITS tree (Fig. 3). As all three accessions appear on long branches, they are delimited as three separate species in both mPTP analyses (Figs 2 & 3). We still regard them as belonging to the same species, since all specimens are morphologically and chemically congruent: they form densely proliferating and imbricate lacinules on adnate squamules with a white prothallus and lack lichen substances. As the species is collected only rarely, we assume that sequencing additional specimens might lead to a better understanding of the possible genetic variation in the species. We were not able to determine the species' closest relative due to poor resolution in the trees, but the ITS and *BEAST trees resolve the species in a clade together with *P. confusa*, *P. mediocris*, *P. neofoliata* and *P. parvifolia*, among others (Figs 3 & 4).

Phyllopsora foliatella Elix

Australas. Lichenol. **58:** 11 (2006, January).—*Psora foliata* var. *subcorallina* Müll. Arg., *Flora* **65:** 483 (1882); type: Australia, Queensland, Toowoomba, *C. H. Hartmann* s. n. (G 00052927—lectotype, designated by Elix (2009): 50, image seen).

Phyllopsora homosekikaica Elix, *Australas. Lichenol.* **59:** 25 (2006, July); type: Australia, Queensland, Mt. Spec State Forest, Paluma Range, 6 km W of Paluma, 19° 01′S, 146°09′E, 920 m alt., on sapling in *Lauraceae-Syzygium*-dominated forest, 18-06-1986, *J. A. Elix & H. Streimann* 20241 (BRI—holotype, not seen: CANB!, O L-1135!—isotypes) (TLC (Elix, on label): homosekikaic acid (submajor), hyperhomosekikaic acid (major); DNA: MK352262 (mtSSU), MK352428 (ITS)).

Descriptions. Elix (2006*c*, as *P. homosekikaica*; 2009, as both *P. foliatella* and *P. homosekikaica*).

Chemistry. Chemotype 1: no lichen substances; chemotype 2: homosekikaic acid

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(major or submajor), hyperhomosekikaic acid (major).

Distribution. Australia.

Discussion. Our study contains two accessions of *P. foliatella* and two of *P. homosekikaica*, including an isotype of the latter. All four accessions group together in a strongly supported clade in the mtSSU tree and are resolved as a single species by mPTP (Fig. 2). As we were unable to generate ITS sequences of *P. foliatella*, the ITS tree contains only the two accessions of *P. homosekikaica*, which also group together with strong support and are resolved as one species (Fig. 3). The two species are morphologically identical, with the isidia developing directly from the prothallus, but differ in their chemistry: *P. foliatella* is acid deficient, while *P. homosekikaica* contains homosekikaic and hyperhomosekikaic acids. Based on the phylogenetic results and the lack of morphological differentiation, we conclude that the species are conspecific and they are synonymized here.

All accessions group into a weakly supported clade with *P. dolichospora* and *P. furfuracea* (Figs 2–4). The three species are characterized by having a light to dark brown prothallus, minute squamules or areoles, and by forming isidia. Their close relationship is therefore quite understandable from a morphological point of view. The two species are readily distinguished from *P. foliatella* by having slightly different spore sizes and by their chemistries: *P. dolichospora* contains furfuraceic acid and a series of related compounds, and *P. furfuracea* contains furfuraceic acid only.

Phyllopsora furfuracea (Pers.) Zahlbr. in Engler

Nat. Pflanzenfam. **1, 1***(225)**:** 138 (1906).—*Lecidea furfuracea* Pers. in Gaudichaud, *Voy. Uranie*: 192 (1827); type: Mariana Islands, *Gaudichaud* s. n. (PC—lectotype, designated by Brako (1991): 46, not seen; H-NYL 20507—isolectotype, not seen).

Lecidea haemophaea Nyl., *Flora* **52:** 122 (1869).—*Phyllopsora haemophaea* (Nyl.) Müll. Arg., *Hedwigia* **34:** 141 (1895); type: Peru, Yurimaguas, *Spruce Lich. Amaz.* 185 (H-NYL 20520—holotype, image seen; BM—isotype, not seen; G 00293371, 00293372—isotypes, images seen) (TLC (Swinscow & Krog 1981): furfuraceic acid (as haemophaea unknown). Synonymy according to Brako (1991)).

Lecidea rhypoderma C. Knight, *Trans. & Proc. New Zealand Inst.* **12:** 375 (1880).—type: New Zealand (not seen) (synonymy according to Zahlbruckner (1925): 761).

Lecidea hypochrysea Vain., *Ann. Acad. Sci. Fenn., Ser. A* **15**(6)**:** 114 (1921).—*Phyllopsora hypochrysea* (Vain.) Swinscow & Krog, *Lichenologist* **13:** 241 (1981); type: Philippines, Mindanao, subprov. Butuan, 320 m, 1911, *Weber* 1393 (TUR-V 22622—holotype, not seen) (TLC (Brako 1991): furfuraceic acid (as furfuracein). Synonymy according to Brako (1991)).

Descriptions. Timdal & Krog (2001), Timdal (2008), Elix (2009).

Chemistry. Furfuraceic acid (major).

Distribution. Pantropical.

Discussion. We include five specimens originally identified as *P. furfuracea* in this study. Surprisingly, they group into two separate, strongly supported clades: three accessions form a clade with *P. dolichospora* and *P. foliatella*, while two accessions are resolved as sister to this clade (Figs 2–4, group A). mPTP resolves the five accessions as belonging to four different species in both analyses (Figs 2 & 3), thus separating all of them except for the ones from Peru and Trinidad and Tobago. All specimens contain furfuraceic acid as chemical compound. Upon closer morphological examination, we found the clade with the accessions from La Réunion, Peru, and Trinidad and Tobago to conform most closely to the current concept of *P. furfuracea*, while the specimens from Ecuador and the Dominican Republic are described as the new species *P. furfurella* (Fig. 5C). See the discussion of *P. furfurella* for further details.

In addition to the five specimens discussed above, we investigated some specimens of the *P. furfuracea* chemotype 2 of Timdal & Krog (2001) and Timdal (2008) (i.e. the acid-deficient strain), but all were resolved to belong in other species, mainly *P. longiuscula*. It is therefore unclear whether an acid-deficient chemical strain of *P. furfuracea* exists. *Phyllopsora furfuracea* is distinguished from the related species *P. dolichospora*, *P. foliatella* and *P. furfurella* either by chemistry (Table 2) and spore size or by having a reddish to dark brown prothallus.

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Phyllopsora furfurella Kistenich & Timdal sp. nov.

MycoBank No.: MB 829274

Differs from *P. furfuracea* in having a white, not reddish brown, prothallus, an orange brown, K+ purple hypothecium containing skyrin, and in details of the mtSSU and ITS sequences.

Type: Ecuador, Loja, Espíndola, buffer zone of Colambo-Yacuri National Park, 4°33′35″S, 79°23′21″W, 2211–2537 m alt., secondary managed forest, regrown after selective or total logging events on primary montane forest, 10 May 2011, *G. Aragón, Y. González, A. Benítez & M. Prieto* (HUTPL!—holotype) (TLC: furfuraceic acid (major), skyrin (in the hypothecium); DNA: MK352189 (mtSSU), MK352361 (ITS)).

(Fig. 5C)

Thallus effuse, crustose; *areoles* minute, granular, up to 0·1 mm diam., scattered or contiguous, pale to medium green, dull, glabrous or slightly pubescent; *isidia c.* 0·1 mm thick, up to 0·4 mm long, simple, more or less straight, pale to medium green, glabrous, adnate to ascending; *upper cortex* poorly defined, formed by 1–2 layers of thin-walled hyphae with rounded lumina, not containing crystals; *medulla* containing crystals dissolving in K; *prothallus* poorly to partly well developed, white.

Apothecia common, up to 1·5 mm diam., round or slightly irregular, sometimes conglomerate, weakly to moderately convex, orange-brown to medium brown, with an indistinct, slightly paler or slightly darker, glabrous margin; *excipulum* orange-brown in inner part, paler at the rim, K+ purple; *hypothecium* orange-brown, K+ purple; *epithecium* colourless; no crystals or granules in the apothecium; *ascospores* narrowly ellipsoid to fusiform, simple, 6·5–9·5 × 2·0–2·5 µm ($n = 30$).

Conidiomata not seen.

Chemistry. Furfuraceic acid (major), skyrin (in the hypothecium).

Etymology. The epithet indicates the morphological resemblance to *P. furfuracea*.

Distribution. Central and South America.

Discussion. The two accessions of *P. furfurella* included in this study were originally named *P. furfuracea* based on the presence of furfuraceic acid, as well as having minute areoles and isidia. The phylogenetic trees, however, reveal the two accessions as a strongly supported group separate from the remaining three accessions of *P. furfuracea* (Figs 2 & 3). Even though the mPTP analyses delimited the two *P. furfurella* accessions as two separate species due to the long branches (Figs 2 & 3), we treat them as one species since both are morphologically similar. They are resolved as sister to the clade consisting of *P. dolichospora*, *P. foliatella* and *P. furfuracea* in the mtSSU and *BEAST trees (Figs 2 & 4), while they are weakly resolved as sister to *P. canoumbrina*, *P. isidiotyla* and one unidentified specimen in the ITS tree (Fig. 3).

Upon closer morphological examination, we found the specimens of *P. furfurella* to have a pure white prothallus, a K+ purple hypothecium due to the presence of skyrin, and slightly smaller ascospores than those of *P. furfuracea*. Two of the three specimens of *P. furfuracea* in our phylogeny did not contain skyrin (hypothecium K–); the third was sterile and hence not examined. We were able to recognize the skyrin-containing taxon after re-examining our material in three further collections of specimens. These were originally identified as *P. furfuracea* from Brazil, Ecuador and Jamaica, although these were not sequenced. Other fertile specimens from the Neotropics, for example those reported from Peru by Timdal (2008), did not contain skyrin, and nor did all examined fertile specimens from the Palaeotropics reported by Timdal & Krog (2001). Assuming that the presence of skyrin in the hypothecium is a diagnostic character for the distinction of the two species, and that the skyrin-containing species is restricted to the Neotropics, we choose to retain the name *P. furfuracea* for the pantropical species.

Additional specimens examined. **Brazil:** *Rio de Janeiro*: Serra da Mantiqueira, Parque National do Itatiaia, 850 m alt., in einem feuchten, dunklen Primärregenwald, 22 vii 1978, *K. Kalb & G. Plöbst*, Kalb, *Lich. Neotropici* No 341 (O L-150058).—**Dominican Republic:** *Puerto Plata*: S of Puerto Plata, Parc National Isabel de Torres, Pico Isabel de Torre, 19°45·73′N, 70°42·68′W, 770 m alt., botanical garden with damp and open forest with mixed trees and shrubs, on palm, 2008, *P. van den Boom* 39069 (hb. v. d. Boom) [DNA: MK352198 (mtSSU), MK352369 (ITS)].—**Ecuador:** *Loja*: Espíndola, upper part of buffer zone of Colambo-Yacuri

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National Park, 4°33′27″S, 79°22′09″W, 2700–2882 m alt., very dense primary montane forest, evergreen, unmanaged and characterized by a dense canopy layer, 10 v 2011, *G. Aragón, Y. González, A. Benítez & M. Prieto* (HUTPL).—**Jamaica:** 'Island of Jamaica', on bark and vegetable debris, 3 iii 1905, *C. E. Cummings*, Merrill, *Lich. Exsicc.* No. 37 (O L-146420).

Phyllopsora glaucella (Vain.) Timdal

Lichenologist **40:** 349 (2008).—*Lecidea breviuscula* var. *glaucella* Vain., *Dansk Bot. Ark.* **4**(11)**:** 21 (1926); type: Mexico, Veracruz, Mirador, 08-1841, *Liebmann* 7381a (TUR-V 34026!—holotype) (TLC: vicanicin, norvicanicin).

Description. Timdal (2008).

Chemistry. Vicanicin, norvicanicin.

Distribution. Central and South America.

Discussion. The four accessions of *P. glaucella* form a strongly supported clade in both phylogenetic trees (Figs 2 & 3) and are resolved as one species in both mPTP analyses (Figs 2 & 3). The species is mainly characterized by the squamulose thallus on a well-developed, reddish brown prothallus, the long, marginal isidia and the chemistry (vicanicin and norvicanicin; Table 2). Based on this combination, it is readily distinguished from other species. The combination of vicanicin and norvicanicin (in addition to zeorin) is also found in the phyllidiate *P. melanoglauca*, which is found in the same large, unresolved clade (Figs 2 & 4).

Phyllopsora gossypina (Sw.) Kistenich *et al.*

Taxon **67:** 894 (2018).—*Lichen gossypinus* Sw., *Prodr.*: 146 (1788).—*Symplocia gossypina* (Sw.) A. Massal., *Neagen. Lich.*: 4 (1854).—*Crocynia gossypina* (Sw.) A. Massal., *Atti Reale Ist. Veneto Sci. Lett. Arti, Ser. 3* **5:** 252 (1860); type: Jamaica, 1784–1786, *O. Swartz* s. n. (UPS L-000259! & L-134473!—syntypes).

Phyllopsora leprosa Riedl, *Oesterr. Bot. Z.* **121:** 145 (1973); type: Surinam, 1827, *Weigel* s. n. (W—holotype, not seen) (synonymy according to Brako (1989)).

Chemistry. Chemotype 1: barbatic acid, divaricatic acid (submajor), two unknown terpenoids (minor); chemotype 2: norstictic acid (major), salazinic acid (major, sometimes absent), unknown compound (minor to trace or absent, R_f classes A:4, B′:6, C:6).

Description. Hue (1909).

Distribution. Pantropical.

Discussion. To our knowledge, only Sipman (2018) has described the chemistry of *P. gossypina* prior to this study. Whereas Sipman (2018) merely lists the main compounds, here we describe two pantropical chemotypes identified in our material. The major compound of chemotype 1 was identified as barbatic acid with divaricatic acid as submajor compound and two unknown terpenoids (minor). The unknown compound of chemotype 2 resembles divaricatic acid in colour and fluorescence and has similar R_f values in solvent systems A and C, but lower R_f value in B′ (moves just below 3-chlorodivaricatic acid).

The six accessions of *P. gossypina* group together in a strongly supported clade and are sister to *P. imshaugii* (Figs 2–4). We were surprised to find these specimens mixed with our accessions of *Crocynia molliuscula*, as well as with the *P. pyxinoides* sequence from GenBank (Fig. 2). All of the chosen *P. gossypina* specimens exhibit an unambiguous *gossypina*-like morphology with a bluish white, felt-like thallus and dark brown apothecia with a lighter margin. As the *P. pyxinoides* sequence from GenBank groups together with a Brazilian specimen of *P. gossypina* chemotype 2 and not with the *P. pyxinoides* specimens identified by us (Fig. 2), we assume that the GenBank specimen is misidentified. See also the discussion for *P. pyxinoides*. *Crocynia mollis* (Nyl.) Nyl. has been regarded as a K+ red variety of *P. gossypina* (Hue 1909; Zahlbruckner 1923), and it is possible that *P. gossypina* chemotype 2 represents that taxon. However, more material of typical *C. mollis* has to be investigated before conclusions can be made.

The two accessions of *C. molliuscula* from La Réunion and Mauritius group together with the Sri Lankan specimen of *P. gossypina* chemotype 1 (Fig. 2). *Crocynia molliuscula* is morphologically distinct from *P. gossypina* in forming small light brown, non-marginate apothecia. While the specimen from La Réunion contains diffractaic acid just as the holotype of *C. molliuscula* (TLC by Kalb, on label attached to H-NYL 22052), the specimen from Mauritius contains norstictic

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acid. Since both specimens of *C. molliuscula* and that of *P. gossypina* from Sri Lanka are from the Palaeotropics in contrast to the other *P. gossypina* accessions in our tree, which are from the Neotropics, it seems as if the topology was resolved according to geography. Still, the apparent morphological differences prevent us from accepting the synonymy of *C. molliuscula* with *P. gossypina* without further investigation. We were able to generate only short sequences of those two specimens and more individuals with a typical *C. molliuscula* morphology and chemistry should be sampled to find out whether *C. molliuscula* is a distinct species or merely a morphologically and chemically deviating form of *P. gossypina*.

mPTP resolves *P. gossypina* as three different species in the mtSSU tree (Fig. 2), while it is delimited as one species in the ITS tree (Fig. 3). This clearly indicates that species of the former genus *Crocynia* need to be investigated more closely. There are no recent taxonomic studies on the former species of *Crocynia*, except for the description of three new species (Lumbsch *et al.* 2011; Aptroot & Cáceres 2014; Sipman 2018) albeit without providing DNA sequences. *Crocynia* is poorly understood and comprises an unnatural assembly of species. The typical felt-like thallus morphology has been shown not to be a taxonomically relevant character at either genus or family level, and it is probable that additional *Crocynia* species belong in *Phyllopsora*.

Phyllopsora halei (Tuck.) Zahlbr.

Cat. Lich. Univ. **4**(3)**:** 398 (1926).—*Pannaria halei* Tuck., *Amer. J. Sci. Arts, Ser. 2* **25:** 424 (1858); type: USA, Louisiana, 1853, *Hale* (FH-TUCK 2828—lectotype, designated by Swinscow & Krog (1981): 241 (as 'holotype', Art. 9.10), not seen; H-NYL 20521!—isolectotype; H-NYL 20522!—isolectotype) (TLC (Timdal & Krog 2001): atranorin, terpenoid T3).

Phyllopsora pannosa Müll. Arg., *Bot. Jahrb. Syst.* **20:** 265 (1895); type: Tanzania, Tanga Prov., Usambara, Kwambugu-Hochwälder, 1894, *C. Holst* 1432 (G—lectotype, designated by Swinscow & Krog (1981): 235, image seen; BM—isolectotype, not seen) (TLC (Swinscow & Krog 1981): atranorin, fatty acids, triterpenoids).

Descriptions. Swinscow & Krog (1981, as *P. pannosa*), Timdal & Krog (2001).

Chemistry. Atranorin (major) and unknown compounds, partly terpenoids (see Timdal & Krog (2001) for characterization of three chemotypes).

Distribution. North America (chemotype 1), Africa (chemotypes 1, 2 and 3), Asia (chemotype 3).

Discussion. Our three accessions of *P. halei* (chemotypes 2 and 3) from the Palaeotropics form a strongly supported clade and are resolved as one species in both mPTP analyses (Figs 2 & 3). They are resolved as sister to the new species *P. amazonica* (Figs 3 & 4) and *P. pyxinoides* (Fig. 4). *Phyllopsora halei* has a characteristic morphology with a thick, reddish brown prothallus, pale green squamules originating from small areoles at the margin of the prothallus, and thick isidia. In combination with chemistry, it is thus readily distinguished from all other known *Phyllopsora* species. The new species *P. amazonica* resembles *P. halei* in forming pale green squamules, isidia and brown-black apothecia, as well as by the presence of atranorin and a series of terpenoids (chemically identical to *P. halei* chemotype 1), but it forms a thinner and less distinct prothallus (see *P. amazonica* for further discussion).

Phyllopsora halei was described from Louisiana and the only published North American collection known to us is the type material. African material of this species was known as *P. pannosa* (e.g. by Swinscow & Krog 1981) until the two species were synonymized by Brako (1991). Whereas the African material is richly isidiate, the American specimens lack isidia (Swinscow & Krog 1981). Unfortunately, we were not able to sequence an American specimen but we agree with Brako (1991) that the species are synonyms because of their otherwise identical morphology, as well as the presence of atranorin and terpenoids.

Phyllopsora himalayensis G. K. Mishra *et al.*

Mycotaxon **115:** 38 (2011): type: India, Himachal Pradesh, Kullu District, Great Himalayan National Park, Shilt, 2800 m alt., on bark, 04-11-2002, *S. Nayaka & R. Srivastava* 02-001037 (LWG—holotype, not seen).

Description. Mishra *et al.* (2011).

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Chemistry. Atranorin.

Distribution. Asia.

Discussion. The species was not studied by us due to the lack of response from LWG to our repeated loan requests. Mishra *et al.* (2011) assumed that the species was close to *P. kalbii* in having globular isidia and a dark brown prothallus. We find several long branches for our *P. kalbii* specimens (Figs 2 & 3), indicating the presence of several (cryptic) species. It would therefore be interesting to generate sequences of *P. himalayensis* and check whether they associate with some of our *P. kalbii* sequences. Some of our unidentified specimens partly fit the description of *P. himalayensis*, but detailed morphological comparisons with the type specimen or sequences are necessary to gain more information about conspecificity.

Phyllopsora hispaniolae Timdal

Biblioth. Lichenol. **106:** 333 (2011); type: Dominican Republic, Prov. Independencia, Sierra de Baoruco, Charco de la Paloma, 48·4 km S of Puerto Escondito, *c.* 18°15′N, 71°36′W, 1800 m alt., humid hardwoods around waterhole, 25-01-1987, *R. C. Harris* 20672 (NY!—holotype) (TLC: argopsin, chlorophyllopsorin).

Description. Timdal (2011).

Chemistry. Argopsin, chlorophyllopsorin.

Distribution. Central and South America.

Discussion. In this study, we include three accessions of *P. hispaniolae*, which form a well-supported clade together with *P. rosei* as sister to *P. nemoralis* (Figs 2–4). Both mPTP analyses resolve *P. hispaniolae* and *P. rosei* to form one entity only (Figs 2 & 3). *Phyllopsora hispaniolae* differs from *P. rosei* in morphology, chemistry and distribution range so we regard it as premature to synonymize these two species. More specimens should be investigated to see whether a morphological and chemical overlap might be observed. See also the discussion under *P. rosei*.

Phyllopsora imshaugii Timdal

Biblioth. Lichenol. **106:** 334 (2011); type: Jamaica, Parish of Portland or St. Thomas, summit of Blue Mt. Peak, 7400 ft alt., 08-10-1952, *H. A. Imshaug* 13037 (MSC 25550!—holotype) (TLC: norstictic acid).

Description. Timdal (2011).

Chemistry. Norstictic acid (major).

Distribution. Central and South America.

Discussion. The three accessions of *P. imshaugii* group together in a strongly supported clade and are resolved as one species in both mPTP analyses (Figs 2 & 3). The specimens are strongly resolved as sister to the byssoid *P. gossypina* (Figs 2–4) but both sit on long and distinct branches (Figs 2 & 3). *Phyllopsora imshaugii* is not byssoid, as it has a distinct upper cortex and forms isidia. The *P. imshaugii* specimen from Ecuador, however, shows a smooth white prothallus with finely pubescent squamules, which may resemble a byssoid thallus on first sight. In addition, *P. imshaugii* forms distinctly marginate apothecia similar to *P. gossypina* and both share the presence of norstictic acid. Thus, the phylogenetic relationship is reflected at least partly in morphology and chemistry.

Phyllopsora isidiosa Kistenich & Timdal sp. nov.

MycoBank No.: MB 829275

Differs from *P. byssiseda* in forming a crustose, areolate thallus and more delicate and branched isidia, and from *P. isidiotyla* in forming less branched, thicker isidia and having a more indistinct and non-pubescent apothecial margin.

Type: USA, North Carolina, Jackson Co., Nantahala National Forest, Chattooga Wild and Scenic River/Ellicot Rock Wilderness, above Fowler Creek, just S of Bull Pen Road, 35°01′08″N, 83°06′12″W, 3000 ft alt., granitic bald on SE-facing slope and adjacent mixed hardwood forest, on *Quercus*, 18 September 2006, *J. C. Lendemer, S. Beeching & A. Moroz* 7765 dupl. (BG L-93867!—holotype) (TLC: no lichen substances; DNA: MK352153 (mtSSU), MK352328 (ITS)).

(Fig. 6A)

Thallus effuse, crustose; *areoles* minute, granular, up to 0·1 mm diam., more or less scattered, pale to medium green, dull, glabrous or slightly pubescent; *isidia c.* 0·1 mm thick, up to 0·8 mm long, simple or branched, more or less straight, pale to medium green, glabrous, adnate to ascending; *upper cortex* poorly defined, up to 15 µm thick, formed

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by a few layers of thin-walled hyphae with rounded lumina (type 2), not containing crystals; *medulla* not containing crystals; *prothallus* usually well developed, white.

Apothecia not common, up to 1 mm diam., round or slightly irregular, mostly simple, weakly to moderately convex, orange-brown to medium brown, when young with an indistinct, slightly paler, glabrous margin; *excipulum* yellowish brown in inner part, paler at the rim, K–; *hypothecium* yellowish brown, K–; *epithecium* colourless; no crystals or granules in the apothecium; *ascospores* narrowly ellipsoid to fusiform, simple, 7·5–11·5 × 2·5–3·0 µm (n = 20).

Conidiomata not seen.

Chemistry. No lichen substances.

Etymology. The epithet indicates that the species is richly isidiate.

Distribution. Pantropical; also occurring in temperate Asia and North America.

Discussion. Initially, specimens of *P. isidiosa* were identified as *P. byssiseda*, albeit being more filigree, but the phylogenetic analyses revealed them to form a separate, strongly supported clade (Figs 2 & 3), which is weakly resolved as sister to the clade containing group A and several other species (Figs 3 & 4, group A). mPTP delimits the accessions as a single species in the mtSSU tree (Fig. 2), while it splits them into four species corresponding to geography in the ITS tree (Fig. 3). The species seems to be widespread, occurring both in tropical and subtropical regions. It is morphologically intermediate between *P. byssiseda* and *P. isidiotyla*, differing from the first in forming a more crustose thallus with more delicate isidia, and from the second in forming somewhat coarser, less branched isidia. It also resembles the new species *P. furfurella* (Fig. 5C) in forming a white prothallus with crustose areoles and isidia. However, *P. furfurella* is readily distinguished by its lichen substances (containing furfuraceic acid in the thallus and skyrin in the hypothecium).

Additional specimens examined. **Australia:** *Queensland*: Girringun National Park, Yamanie Section, 14 km WNW of Abergowrie, remnant rainforest along Herbert River, 18°24′49″S, 145°46′18″E, 55 m alt., on trunk of treelet, 2006, *J. A. Elix* 38478 (CANB 798838) [DNA: MK352267 (mtSSU), MK352433 (ITS)].—**Brazil:** *Mato Grosso do Sul*: etwa 30 km südlich von Campo Grande, 550 m, in einem dichten cerrado, 14 xi 1979, *K. Kalb & G. Plöbst*, Kalb, *Lich. Neotrop. Exsicc.* 343 (B 60-156328). *São Paulo*: Município de Mogi-Gauçu, Distrito de Martinho Prado Jt., Reserva Ecológica de Mogi-Guaçu, cerrado between gravel road and 'pau brasil' plantation, 2007, *R. Lücking & E. Rivas Plata* 23302 (SP 393465) [DNA: MG925907 (mtSSU), MG926004 (ITS)].—**Dominican Republic:** *Puerto Plata*: S of Puerto Plata, Parc National Isabel de Torres, Pico Isabel de Torre, 19°45·73′N, 70°42·68′W, 770 m alt., botanical garden with damp and open forest with mixed trees and shrubs, on *Spathodea campanulata*, 2008, *P. van den Boom* 39012 (hb. v. d. Boom) [DNA: MK352197 (mtSSU), MK352368 (ITS)]; *ibid.*, on big tree, *P. van den Boom* 39074 (hb. v. d. Boom).—**Indonesia:** *West Java*: Cibodas, Botanical Garden, *c.* 1400 m alt., on tree, 2003, *L. Sudirman & H. Sipman* 51474 (B 60-168671).—**Malaysia:** *Sabah*: Malaysian Borneo, SAFE-Project area, mostly *Macaranga*-dominated secondary forest, 2012, *P. Wolseley, H. Thüs & C. Vairappan* S.P.5 (BORH).—**Nepal:** from Thulo Syabru to Bamboo, Machilus, 1800 m alt., 2007, *L. R. Sharma* et al. M16 (E 305556) [DNA: MK352155 (mtSSU), MK352330 (ITS)]; from Thulo Syabru to Bamboo, river/suspension bridge, 28°08′34″N, 85°22′11″E, 2000 m alt., on *Castanopsis* tree trunk, low temperate mixed broad-leaved forest, 2007, *L. R. Sharma* et al. L25-2 (E 305558).—**Philippines:** *Laguna Province*: Luzon, Los Baños, Mount Makiling Forest Reserve, 14°08′N, 121°14′E, 370 m alt., parkland close to the university, corticolous, 1994, *P. Diederich* 13210 (hb. Diederich) [DNA: MK352232 (mtSSU)].—**Thailand:** *Chiang Mai*: Doi Suthep, King's Palace, 18°49′N, 99°53′E, 1550 m alt., oak/chestnut forest, 1991, *P. A. Wolseley & B. Aguirre-Hudson* 5552 (BM 749822).—**USA:** *South Carolina*: Darlington Co., S edge of Louthers Lake (oxbow lake W of Great Pee Dee River), 34°18′05″N, 79°42′42″W, *c.* 30 m alt., large Stream Swamp (cypress forest) on lake shore, partly shaded, on *Taxodium distichens* trunk, 2008, *G. B. Perlmutter, S. Q. Beeching & M. F. Hodges* 1598 (NY); Macon Co., Bank of Chattooga River, near the 3-state corner, 35°00′N, 83°06′W, 630 m alt., on trunk of *Magnolia fraseri* in thick *Rhododendron* thickets, 1995, *A. Nordin* 4187 (UPS L-71532).

Phyllopsora isidiotyla (Vain.) Riddle

Mycologia **15:** 81 (1923).—*Lecidea isidiotyla* Vain., *Acta Soc. Fauna Fl. Fenn.* 7(2)**:** 49 (1890); type: Brazil, Minas Gerais, Lafayette, 1885, *E. A. Wainio, Lich. Bras. Exs.* 222 (TUR-V 22634!—lectotype, designated by Swinscow & Krog (1981): 242 (as 'holotype', Art. 9.10); BM, M, UPS, ZT—isolectotypes, not seen) (TLC: atranorin (major), zeorin (major)).

Descriptions. Brako (1991), Elix (2009).

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Chemistry. Atranorin, zeorin; possibly also acid deficient (see below).

Distribution. Brazil; reports from elsewhere require confirmation.

Discussion. We were able to sequence only one specimen considered to be *P. isidiotyla* in this study. The accession is resolved as sister to *P. canoumbrina* (Figs 2–4), from which it differs by forming small, branched isidia. It is delimited as a single species in both mPTP analyses (Figs 2 & 3). Even though *P. isidiotyla* is supposedly widespread (e.g. Brako 1991; Elix 2009; Mishra *et al.* 2011), it proved difficult to obtain material that could be unambiguously identified as *P. isidiotyla*. The holotype contains major amounts of zeorin (and atranorin) but we have found zeorin in *Phyllopsora* only in *P. buettneri*, *P. melanoglauca*, *P. neotinica*, *P. porphyromelaena* and *P. subhispidula*, species that differ markedly from *P. isidiotyla* in morphology. Our specimen representing *P. isidiotyla* in the phylogenetic analyses is from Brazil and resembles the holotype in morphology but lacks the lichen substances. We regard all published reports of *P. isidiotyla* as doubtful and recommend sequencing more specimens to investigate the full morphological and geographical extent of this species.

Phyllopsora kalbii Brako

Fl. Neotrop. Monogr. **55:** 51 (1991); type: Brazil, Mato Grosso do Sul, Estrada do Pantanal, some kms E of Coxim, 270 m alt., 29-06-1980, *K. Kalb* 250 p.p. (NY—holotype, not seen).

Descriptions. Brako (1991), Timdal & Krog (2001).

Chemistry. Atranorin (minor to trace) or no lichen substances.

Distribution. North, Central and South America, Africa, Asia.

Discussion. All accessions of *P. kalbii* form a strongly supported clade in both phylogenies but are delimited as several species in the mPTP analyses (Figs 2 & 3). All specimens appear on very long branches, particularly in the ITS tree (Fig. 3), most likely because of highly variable ITS1 sequences in all specimens. The palaeotropical and South American specimens group together respectively, while the position of the North American specimen varies (Figs 2 & 3). However, all specimens are morphologically similar, having small, pale green squamules growing on a thin white prothallus and short globular isidia, and they lack lichen substances (or contain small amounts of atranorin). Hence, we consider them to belong to the same species, although more specimens from additional geographical regions are likely to provide better resolution. *Phyllopsora kalbii* is resolved as sister to *P. cuyabensis* in a clade with *P. byssiseda* and *P. fendleri* (Figs 2 & 4). It differs from *P. cuyabensis* in, for example, forming an upper cortex and from *P. byssiseda* and *P. fendleri* in forming smaller squamules and a thinner prothallus. *Phyllopsora kalbii* might also be confused with *P. corallina* based on morphology, but the latter differs in having long and cylindrical isidia. Mishra *et al.* (2011) considered *P. himalayensis* to be a close relative of *P. kalbii*; unfortunately, we were not able to sequence that species.

Phyllopsora loekoesii S. Y. Kondr. *et al.*

Acta Bot. Hung. **58:** 349 (2016); type: Korea, Gyeongsangbuk-do, Ulleung-gun, Ulleung-eup, between Naesujeon and Soekpo waterfall, 37° 31′19·51″N, 130°54′16·03″E, 415 m alt., at a rock wall, on siliceous rocks, 09-07-2016, *S. Y. Kondratyuk & L. Lökös* 161759 (Korean Lichen Research Institute 39977!—holotype).

Description. Kondratyuk *et al.* (2016).

Chemistry. No lichen substances.

Distribution. Asia.

Discussion. The two accessions of *P. loekoesii* group together in a supported clade in both analyses and are revealed as sister to *P. confusa* (Figs 2–4). The two specimens are recovered as two separate species in the mPTP analyses (Figs 2 & 3) but cluster together with unpublished sequences by Kondratyuk of the holo- and isotype in a separate phylogenetic analysis (data not shown). The two specimens are morphologically similar and therefore we choose to treat them as

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the same species despite the mPTP results. In morphology, *P. loekoesii* is highly similar to its sister species *P. confusa*. Both have small squamules and do not contain lichen substances, but *P. loekoesii* differs from *P. confusa* in forming isidia (vs. lacinules) and having longer ascospores.

The species is new to Japan and Nepal.

Phyllopsora longiuscula (Nyl.) Zahlbr.

Cat. Lich. Univ. **4**(3)**:** 398 (1926).—*Lecidea longiuscula* Nyl., *Ann. Sci. Nat., Bot., Sér. 4* **19:** 339 (1863); type: Cuba, s. loc., *C. Wright* s. n. (H-NYL 20537!—lectotype, designated by Swinscow & Krog (1981): 242; BM!, UPS L-108157!—isolectotypes, issued as Tuckerman, *Wright Lich. Cub*. No. 179) (TLC: no lichen substances).

Lecidea intermediella Nyl., *Ann. Sci. Nat., Bot., Sér. 4* **19:** 339 (1863).—*Phyllopsora intermediella* (Nyl.) Zahlbr., *Cat. Lich. Univ.* **4**(3)**:** 398 (1926); type: Cuba, s. loc., *C. Wright* s. n. (H-NYL 20558!—lectotype, designated by Brako (1991): 49 (as 'holotype', Art. 9.10); BM!, UPS L-108152!—isolectotypes, issued as Tuckerman, *Wright Lich. Cub*. No. 183) (TLC (Brako 1991): no lichen substances).

Description. Brako (1991).

Chemistry. No lichen substances.

Distribution. Central and South America, Asia, Australia.

Discussion. When selecting specimens for this study, we struggled to find correctly identified specimens of *P. intermediella*, some being misidentified. When investigating the holotypes of both species, we found them to be strikingly similar in morphology. The main difference is that *P. intermediella* forms isidia while *P. longiuscula* forms lacinules, and also the ascospores are reported to be shorter in the former species. Many specimens of *P. intermediella* were collected from rocks, which is highly unusual in *Phyllopsora*. We have only once encountered a saxicolous, typical (i.e. lacinulate) *P. longiuscula* specimen, sequenced here as specimen 1039. In our phylogeny (Figs 2 & 3) the sequence of an isidiate specimen (454) is nested within a clade of lacinulate specimens (467, 1039, 6761).

Isidia are generally common in *Phyllopsora* species and Brako (1991) found the presence or absence of isidia to be an unreliable taxonomic character. It is possible that the presence of isidia or lacinules depends on ecological factors. Other species, for example *P. breviuscula*, also show a generally wide morphological variability. Even though ascospores are reported to be longer in *P. longiuscula*, we suspect that this character is unreliable in this case, as only a small number of spores have been measured.

As all of the four accessions used in this study group together in a supported clade (Figs 2 & 3), we consider them to belong to the same species and synonymize *P. intermediella* with *P. longiuscula*. Additional, unpublished but incomplete sequences of *P. intermediella* specimens support this decision. However, mPTP suggests that the specimens belong to several species due to the long branches (Figs 2 & 3). The closest relatives of *P. longiuscula* seem to be *P. breviuscula* and *P. mauritiana* (Figs 2 & 4), from which it differs by forming smaller squamules and vegetative propagules (lacinules or isidia).

The species is new to Australia (New South Wales, *Elix* 42451, CANB).

Phyllopsora malcolmii Vězda & Kalb

In Vězda, *Lich. Rar. Exsicc.* **20:** 4 (1995); type: New Zealand, South Island, Nelson, loco 'Brook Stream track' dicto, ad corticem arborum, 120 m alt., 23-05-1994, *W. Malcolm* s. n., Vězda, *Lich. Rar. Exs.* 200 (CHR—holotype, not seen; BM!, GZU!—isotypes) (TLC: no lichen substances; DNA: MK352170 (mtSSU), MK352344 (ITS)).

Description. Galloway (2007).

Chemistry. No lichen substances.

Distribution. New Zealand.

Discussion. The species is known only from the type collection and we were able to generate sequences from an isotype. The accession is resolved differently in the two trees: in the mtSSU and *BEAST trees (Figs 2 & 4) it is the sister to the unidentified specimen 7227 from Sri Lanka in a clade with *P. canoumbrina*, *P. isidiotyla* and additional unidentified specimens. In the ITS tree (Fig. 3), in contrast, it falls into group A as sister to *P. dolichospora*, *P. foliatella* and *P. furfuracea*. *Phyllopsora malcolmii* seems to be closely associated to the unidentified specimen

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Phyllopsora sp. (7227) from Sri Lanka but is resolved as a distinct species in the mPTP analyses (Figs 2 & 3). The two specimens differ morphologically, since *P. malcolmii* has a marked white prothallus with arachnoid hyphae whereas the Sri Lankan specimen has flat adnate squamules when young, growing into small coralloid squamules when older. Argopsin (reported in the protologue) was not detected by us in the isotype and specimen 7227 is also acid deficient.

Phyllopsora martinii Swinscow & Krog

Lichenologist **13:** 232 (1981); type: Kenya, Coast Province, Kwale District, Shimba Hills, 25 km SW of Mombasa, Kivumoni Forest, tree trunk in shady forest, rather dry, 02-1972, *T. D. V. Swinscow & H. Krog* K42/3 (BM—holotype, not seen; O L-1144!—isotype) (TLC: argopsin, chlorophyllopsorin, norargopsin).

Descriptions. Swinscow & Krog (1981), Timdal & Krog (2001).

Chemistry. Argopsin (major), chlorophyllopsorin (major), norargopsin (minor).

Distribution. Africa.

Discussion. The two accessions of *P. martinii* cluster together with strong support and are resolved as a single species in both mPTP analyses (Figs 2 & 3). *Phyllopsora martinii* is morphologically similar to *P. corallina* with its medium-sized squamules and isidia, but can be distinguished by the shorter ascospores and the chemistry (argopsin, chlorophyllopsorin and norargopsin in *P. martinii* vs. no lichen substances in *P. corallina*).

Phyllopsora mauritiana (Taylor) Swinscow & Krog

Lichenologist **13:** 242 (1981).—*Lecidea mauritiana* Taylor, *London J. Bot.* **6:** 151 (1847); type: Mauritius, s. loc. (FH—lectotype, designated by Swinscow & Krog (1981): 242, not seen) (TLC (Swinscow & Krog 1981): no lichen substances).

Description. Timdal & Krog (2001).

Chemistry. No lichen substances.

Distribution. Africa.

Discussion. The three accessions of *P. mauritiana* group into a strongly supported clade in both phylogenetic trees (Figs 2 & 3) and as sister to *P. breviuscula* (Figs 2–4). They are delimited as a single species in the ITS mPTP analysis (Fig. 3). In the mtSSU tree, mPTP splits the accessions into two species (Fig. 2), most likely due to long branches. The species is characterized by the crustose thallus, which is formed by discrete to adjoining areoles on a thick, reddish brown prothallus, the absence of vegetative dispersal units and lack of lichen substances. Thus, its phylogenetic sister-relationship to *P. breviuscula* (Figs 2–4) is also reflected in morphology and chemistry: both lack lichen substances and vegetative dispersal units. In addition, it resembles the neotropical morphotype of *P. breviuscula* in forming a dense prothallus with flat, pubescent squamules, but is distinguished by its squamules being more adnate, isodiametric and more crust-like than those of *P. breviuscula*.

Phyllopsora mediocris Swinscow & Krog

Lichenologist **13:** 234 (1981); type: Tanzania, Tanga Province, Usambara Mountains, Amani, near Forestry House, alt. *c.* 900 m, 5°07′S, 38°38′E, 09-01-1971, *R. Moberg* 1481a-1 (UPS L-10381!—holotype) (TLC (Swinscow & Krog 1981): no lichen substances).

Descriptions. Swinscow & Krog (1981), Timdal & Krog (2001).

Chemistry. No lichen substances.

Distribution. Africa, Asia.

Discussion. The three accessions of *P. mediocris* are resolved in a strongly supported clade as sister to *P. parvifolia* (Figs 2–4) and delimited as one species in both mPTP analyses (Figs 2 & 3). The species is readily distinguished from other species of *Phyllopsora* by the medium-sized, soon ascending squamules on a medium thick, reddish brown prothallus, simple lacinules and the lack of lichen substances. The sister species, *P. parvifolia*, also lacks lichen substances but forms a more rosulate thallus and phyllidia.

Phyllopsora melanoglauca Zahlbr.

Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. **83:** 133 (1909); type: Brazil, São Paulo, in silvaticis

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prope urbem Iguape, 20–100 m alt., 09-1901, *V. Schiffner* s. n. (W—lectotype, designated by Swinscow & Krog (1981): 242 (as 'holotype', Art. 9.10), not seen; BM!—isolectotype) (TLC: vicanicin, zeorin).

Descriptions. Brako (1991, as *P. buettneri* var. *glauca* chemotype I) and Timdal (2008, as *P. buettneri* chemotype 3).

Chemistry. Vicanicin (major), norvicanicin (minor, trace, or absent), zeorin (major).

Distribution. Neotropical; palaeotropical records need confirmation.

Discussion. We include five specimens of *P. buettneri* chemotype 3 in this study. They group together in a strongly supported clade and are resolved as a separate species not closely related to the remaining chemotypes of *P. buettneri* (Figs 2 & 3). We therefore conclude that they comprise a distinct species and resurrect the old name *P. melanoglauca* for this taxon. Unfortunately, we were not able to resolve the closest sister to *P. melanoglauca* in either tree (Figs 2–4). The species is morphologically identical to *P. buettneri* but can be readily distinguished by its chemistry, containing vicanicin, zeorin, and often norvicanicin. Vicanicin and norvicanicin are also found in *P. glaucella*, which might be a close relative and occurs in the same larger clade. All specimens we have examined of *P. melanoglauca* are from the Neotropics. See also *P. buettneri* and the Discussion for more information.

Phyllopsora methoxymicareica Elix

Australas. Lichenol. **59:** 25 (2006); type: Australia, New South Wales, Clyde Mountain, below the road, 20 km SE of Braidwood, 35°35′S, 149°57′E, 700 m alt., in wet sclerophyll forest on base of *Eucalyptus vimialis*, 14-02-1989, *J. A. Elix* 22773 (CANB 743017—holotype, fragment seen).

Descriptions. Elix (2006*c*, 2009).

Chemistry. Methoxymicareic acid (major), hydromicareic acid (trace) (Elix 2009).

Distribution. Australia.

Discussion. We were unable to generate sequences from a fragment of the holotype sent to us, despite it being only 29 years old. The species resembles *P. furfuracea* and *P. foliatella* as all three species have a crustose, areolate thallus and form numerous isidia, but they differ in spore size and chemistry (Table 2). Sequencing fresh specimens is necessary in order to draw further conclusions. *Phyllopsora methoxymicareica* is best identified by its characteristic chemistry.

Phyllopsora microdactyla (C. Knight) D. J. Galloway

New Zealand J. Bot. **21:** 196 (1983).—*Lecidea microdactyla* C. Knight, *Trans. & Proc. New Zealand Inst.* **12:** 375 (1880); type: New Zealand, s. loc., *C. Knight* (BM—lectotype, designated by Galloway (1983): 196, not seen; H!—three probable isolectotypes) [TLC: no lichen substances].

Lecidea carpodeti Zahlbr., *Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Kl.* **104:** 308 (1941); type: New Zealand, Otago, Dunedin, Boyd's Bush, *J. S. Thomson* T 492 (ZA 566) (CHR 347017—lectotype, designated by Galloway (1983): 196, not seen; BM!—isolectotype).

Parmeliella mucorina Zahlbr., *Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Kl.* **104:** 272 (1941); type: New Zealand, Wellington, Greatford, on *Melicytus ramiflorus*, 07-1933, *H. H Allan* 138 (W 2304—holotype, not seen) (synonymy based on Galloway (1985) and Jørgensen (2003)).

Description. Galloway (1985).

Chemistry. No lichen substances.

Distribution. New Zealand.

Discussion. We know of no reliably identified, recently collected material of *P. microdactyla*, and did not attempt to extract DNA from the old, probable isolectotypes in H. The species is characterized by coralloid, granular to microphylline squamules on a pale prothallus, cylindrical isidia, large ascospores and the absence of lichen substances. Some of the unidentified *Phyllopsora* specimens from Malaysia and Sri Lanka resemble this species but differ, for example, in having dark brown, more distinctly marginate apothecia. As we have no information regarding the extent of the morphological variability in *P. microdactyla*, sequences of the type material or of freshly collected material from the type locality are essential for gaining information about the species' phylogenetic relationships.

Phyllopsora nemoralis Timdal & Krog

Mycotaxon **77:** 85 (2001); type: La Réunion, Forêt de Bélouve, track from Gite de Bélouve to viewpoint, 21°

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03′S, 55°32′E, 1500–1550 m alt., 30-09-1996, *H. Krog & E. Timdal* RE25/32 (O L-867!—holotype) (TLC: argopsin, atranorin; DNA: MK352142 (mtSSU)).

Description. Timdal & Krog (2001).

Chemistry. Argopsin (major) and atranorin (minor).

Distribution. Africa.

Discussion. The two accessions of *P. nemoralis*, including the holotype, cluster together in a strongly supported clade in the mtSSU tree (Fig. 2). Both mPTP analyses delimit *P. nemoralis* as a separate species, which is sister to the *hispaniolae-rosei* complex (Figs 2–4). Several of our specimens, which were identified as *P. nemoralis*, were found to belong to other species by molecular data, such as *P. confusa*, while the specimen from South Africa was initially named *P. hispaniolae*. This indicates the morphological similarity of *P. nemoralis* with its sister clade. Indeed, all three species, *P. hispaniolae*, *P. nemoralis* and *P. rosei*, share the presence of argopsin and form ascospores of a similar size. However, thallus morphology, vegetative dispersal units, colour of the prothallus, and additional minor compounds are slightly different between the species. *Phyllopsora nemoralis* is the only species forming isidia and containing atranorin in addition to argopsin.

Phyllopsora neofoliata Elix

Australas. Lichenol. **59:** 26 (2006); type: Australia, New South Wales, Lord Howe Island, Max Nicholls Track, 31°31′08″S, 159°03′03″E, 5 m alt., on tree in lowland forest, 20-06-1992, *J. A. Elix* 32714 (CANB 740185—holotype, not seen; O L-1319!—isotype, fragment) (DNA: MK352263 (mtSSU), MK352429 (ITS)).

Descriptions. Elix (2006*c*, 2009).

Chemistry. Furfuraceic acid (major), ± physodic acid (minor or trace) (Elix 2006*c*, 2009).

Distribution. Africa, Australia.

Discussion. The three accessions of *P. neofoliata* group together in a strongly supported clade and are resolved as a single species in both mPTP analyses (Figs 2 & 3). Its sister species could not be resolved in either phylogenetic tree, but *P. neofoliata* is found in a larger clade with *P. castaneocincta*, *P. confusa*, *P. mediocris* and *P. parvifolia* among others (Figs 2–4). The chemistry can be similar to *P. castaneocincta* (furfuraceic acid) but may also contain physodic acid as minor to trace (Elix 2006*c*). The specimen from Kenya, however, seems to represent an acid-deficient strain, since it did not contain any lichen substances when investigated by TLC. That specimen also differs slightly in morphology from the Australian specimens by forming narrower squamules and a brownish prothallus. We assume this to be due to geographical variation within the species. It was named *neofoliata* because of its similarity to *P. foliata* (Elix 2006*c*). That species occurs in the same larger clade (Figs 3 & 4) although it is uncertain to what degree the species are related.

The species is new to Africa (Kenya).

Phyllopsora neotinica Kistenich & Timdal sp. nov.

MycoBank No.: MB 829276

Differs from *P. chodatinica* in containing argopsin and often zeorin, and apparently lacking chodatin.

Type: Venezuela, Capital District, Parque Nacional Macarao, 1·5 km E of El Junquito, 10°27·50′N, 67° 04·52′W, 1880 m alt., tree trunk in tropical moist forest, 0–3 m above ground, trunk diam. 20 cm, 12 November 2015, *M. S. Dahl, J. E. Hernández M., S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-246 (O L-202526!—holotype; VEN!—isotype) (TLC: argopsin (major), unknown xanthone (major), zeorin (trace); DNA: MK352215 (mtSSU), MK352386 (ITS)).

(Fig. 6B)

Thallus effuse, squamulose; squamules medium-sized to large, ascending, elongated, often imbricate, incised to deeply divided, plane to weakly convex; upper side yellowish green, glabrous, epruinose; *margin* concolorous with upper side or somewhat paler, finely pubescent; lacinules numerous, developing from lobe-tips; *upper cortex* of type 1, 25–40 µm thick, containing a few crystals dissolving in K (PD–, K–); *medulla* containing crystals dissolving in K (PD+ orange or PD–, K–); *prothallus* usually well developed, reddish brown.

Apothecia seen in one collection, up to 1·2 mm diam., rounded, simple or slightly

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conglomerate, weakly to moderately convex, reddish brown, with an indistinct and often darker margin; *excipulum* reddish brown (K+ faintly purple), darkest near the rim; *hypothecium* pale brown; *epithecium* colourless; apothecium containing scattered groups of orange crystals dissolving in K (K+ yellow); *ascospores* narrowly ellipsoid to fusiform, simple, 5–8 × 2·0–2·5 µm ($n = 20$, from a single apothecium).

Conidiomata not seen.

Chemistry. Argopsin (major, rarely absent), unknown xanthone (major) and zeorin (minor to trace, or rarely absent).

Etymology. The epithet is a contraction of 'the neotropical *Phyllopsora chodatinica*'.

Distribution. North, Central and South America.

Discussion. The five accessions of *P. neotinica* were initially named *P. chodatinica*. They are resolved with strong support within the clade *P. buettneri-chodatinica-porphyromelaena* and *P. chlorophaea* (Fig. 4). The mPTP analyses resolve the accessions as a species distinct from *P. chodatinica* (Figs 2 & 3). *Phyllopsora neotinica* was first thought to be a chemical variety of *P. chodatinica* occurring in the Neotropics. It is morphologically identical to *P. chodatinica* but differs in its chemical compounds: *Phyllopsora neotinica* usually contains argopsin and zeorin in addition to an unknown xanthone, although apparently not chodatin, whereas *P. chodatinica* contains only xanthones, including chodatin. Sequences from the paratype of *P. chodatinica* turned out to be invaluable for fixing the name *chodatinica* to the correct clade. The possible substitution of chodatin by a xanthone with very similar R_f values in the neotropical '*P. chodatinica*' was discussed by Timdal (2008). We assume that most or all of the species records of *P. buettneri* var. *glauca* chemotype II in Brako (1991), as well as all neotropical *P. chodatinica* specimens in Timdal (2008, 2011), belong to *P. neotinica*. See also discussion under *P. chodatinica* for more details.

Selected specimens examined. **Brazil:** *Rio de Janeiro*: Parque Nacional do Itatiaia, surroundings of Abrigo Lamego, 22°25·63′S, 44°37·23′W, 1150 m alt., on tree trunk in Atlantic rainforest, 2015, *M. S. Dahl, S. Kistenich, E. Timdal & A. K. Toreskaas* SK1-402 (O L-202682) [DNA: MK352222 (mtSSU), MK352393 (ITS)].—**Costa Rica:** *Puntarenas Prov.*: Esquinas rainforest area SW of the village La Gamba (*c.* 8 km NNW of Golfito), ridge S above the field station 'Tropenstation La Gamba', along the trail from the field station into the Valle Bonito tropical lowland rainforest, 8°42′10″N, 83°12′30″W, 200 m alt., on rough bark of evergreen trees, 2003, *J. Hafellner & B. Emmerer* 1247 (GZU).—**Cuba:** *Pinar del Rio*: Reserva de la Biosfera Sierra del Rosario, S side of "Loma el Salón", 22°49·74′N, 82°57·89′W, 500–510 m alt., corticolous on trunk of unidentified tree in mixed hardwood forest on N-facing slope near crest, 2007, *T. Tønsberg* 37923 (BG L-89975) [DNA: MK352149 (mtSSU), MK352324 (ITS)].—**Dominica:** *St. David*: Parish of St. David, L'Or, 1000 ft alt., rainforest, 1963, *F. H. Imshaug & H. A. Imshaug* 33186 (MSC 25592).—**Dominican Republic:** *La Vega*: La Sal, 13·3 km N of El Río, then 10 km E of Paso Bajito, on road to Casabito, 3500–3600 m alt., humid hardwoods along stream, 1982, *R. C. Harris* 15005 (NY).—**Guatemala:** *Baja Verapaz*: SSE of Coban, SE of Purulhá, Biotopo Mario Dary Rivera (Biotopo del Quetzal), 'Fern Trail', 15°13·5′N, 90°13·6′W, 1700 m alt., NE exposed slope with tropical rainforest, 2004, *P. van den Boom* 33395 (immixture) (hb. v. d. Boom).—**Jamaica:** *Portland*: Parish of Portland, Moodies Gap Trail near Hardwar Gap, Blue Mountains, 3800 ft alt., 1952, *H. A. Imshaug* 13101 (MSC 25514).—**Peru:** *San Martin*: Cerro Escalera (*c.* 20 km, road distance, NE of Tarapoto), 6°27′S, 76°15′W, 900–1100 m alt., 1981, *R. Santesson & G. Thor* P72:20 (S).—**Puerto Rico:** *Humacao*: Caribbean National Forest, Luquillo Division, Mt. El Toro, trail from El Verde side on Hwy 186, 850 m alt., 1988, *R. C. Harris* 22248 (NY).—**St. Lucia:** Mt. Casteau, Quarter of Soufriére, 2000–2000 ft alt., 1963, *F. H. Imshaug & H. A. Imshaug* 29810 (MSC 25633).—**St. Vincent and the Grenadines:** *St. Vincent*: Bow Woods, 800 ft alt., on trees, 1896, *W. R. Elliot* 135 (BM).—**Trinidad and Tobago:** *Tobago*: Parish of St. Paul, along Roxborough Parlatuvier Road, 11°16·81′N, 60°36·64′W, 500–520 m alt., on tree trunk in rainforest, 2008, *S. Rui & E. Timdal* 10763 (O L-152060) [DNA: MK352176 (mtSSU), MK352349 (ITS)]; same site, 11°17·04′N, 60°35·69′W, 400–450 m alt., on tree trunk in rainforest, 2008, *S. Rui & E. Timdal* 10774 (O L-152071) [DNA: MK352137 (mtSSU), MK352316 (ITS)].—**USA:** *Florida*: Wakulla County Apalachicola National Forest, along Forest Serv. Rd 309 at Lost Creek just S of Leon Co. line, 5·6 mi W of Florida Hwy 267, swamp forest, on *Fraxinus*, 1988, *R. C. Harris* 23375 (NY).

Phyllopsora ochroxantha (Nyl.) Zahlbr.

Cat. Lich. Univ. **10** (24)**:** 377 (1939).—*Lecidea ochroxantha* Nyl., *Ann. Sci. Nat., Bot., Sér. 4* **11:** 223 (1859); type: Bolivia, Campolican, *Weddell* s. n. (H-NYL 20489!—lectotype, designated by Swinscow & Krog

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(1981): 243; H 9504194—isolectotype, image seen; PC—isolectotype, not seen) (TLC: phyllopsorin, chlorophyllopsorin).

Lecidea subvirescens Nyl., *Ann. Sci. Nat., Bot., Sér. 5* **7:** 321 (1867).—*Phyllopsora subvirescens* (Nyl.) Swinscow & Krog, *Lichenologist* **13:** 240 (1981); type: Colombia, Nova Granata, Rio Negro, 1200 m alt., 1863, *Lindig* s. n. (H-NYL 20492—holotype, image seen) (TLC (Brako 1991): phyllopsorin, chlorophyllopsorin; synonymy according to Brako (1989, 1991)).

Lecidea ernstiana Müll. Arg., *Flora* **60:** 473 (1877).—*Phyllopsora ernstiana* (Müll. Arg.) Müll. Arg., *Bot. Jahrb. Syst.* **20:** 265 (1895); type: Venezuela, Caracas, *Ernst* 190 (G 00293369—holotype, image seen) (TLC (Swinscow & Krog 1981): phyllopsorin, chlorophyllopsorin (as ochroxantha unknowns 1 and 2). Synonymy according to Swinsow & Krog (1981) and Brako (1989, 1991)).

Psora polydactyla Müll. Arg., *Flora* **70:** 320 (1887).—*Phyllopsora polydactyla* (Müll. Arg.) Zahlbr., *Cat. Lich. Univ.* **4**(3)**:** 400 (1926); type: Brazil, São Paulo, Apiahy, 04-1882, *Puiggari* 2156 (G 00293370—holotype, image seen) (TLC (Brako 1991): argopsin, phyllopsorin, chlorophyllopsorin. Synonymy according to Brako (1989, 1991)).

Lecidea spinulosa Vain., *Acta Soc. Fauna Fl. Fenn.* **7**(2)**:** 46 (1890).—*Phyllopsora spinulosa* (Vain.) Zahlbr., *Cat. Lich. Univ.* **4**(3)**:** 401 (1926); type: Brazil, Minas Geraës, Sitio, 1885, *E. A. Wainio, Lich. Brasil. Exsicc.* 993 (TUR-V 22627—lectotype, designated by Swinscow & Krog (1981): 245 (as 'holotype', Art. 9.10), not seen; BM!—isolectotype, issued as Vainio, *Lich. Brasil. Exs.* No. 993) (TLC: phyllopsorin, chlorophyllopsorin and two unknown compounds).

Lecidea glabriuscula Nyl., *Sert. Lich. Trop.*: 40 (1891).—*Phyllopsora glabriuscula* (Nyl.) Swinscow & Krog, *Lichenologist* **13:** 241 (1981); type: Cuba, s. loc., *C. Wright Lich. Cub.* ser. 2, 105 (H-NYL 20534!—holotype; FH-TUCK 2922—isotype, not seen, issued as Tuckerman, *Wright Lich. Cub.*, ser. 2, 105) (TLC: phyllopsorin, chlorophyllopsorin).

Descriptions. Timdal (2008), Elix (2009).

Chemistry. Phyllopsorin (major), chlorophyllopsorin (major to minor), argopsin (occasional trace), norargopsin (occasional trace) and unknown compounds (occasional traces).

Distribution. Neotropical; palaeotropical records require confirmation.

Discussion. The five accessions of *P. ochroxantha* cluster together in a strongly supported clade (Figs 2 & 3). The mtSSU mPTP analysis resolves all accessions as a single species (Fig. 2) while the ITS analysis splits the accessions from Brazil as well as Trinidad and Tobago as separate species (Fig. 3). The Caribbean specimen appears on a long branch in the ITS tree (Fig. 3) whereas the branch is considerably shorter in the mtSSU tree (Fig. 2). As this specimen agrees with the remaining specimens in morphology and chemistry, we consider that all of them belong to *P. ochroxantha*. The species is sister to the *africana-swinscowii* clade (Figs 2–4, group C). *Phyllopsora ochroxantha* is distinguished from its two morphological and phylogenetic sister species only by its main chemical compounds (chlorophyllopsorin and phyllopsorin in *P. ochroxantha* vs. various combinations of argopsin, chlorophyllopsorin, methyl 2,7-dichloropsoromate and methyl 2,7-dichloronorpsoromate in the two other species). See *P. africana* and Discussion for further details.

Phyllopsora parvifolia (Pers.) Müll. Arg.

Bull. Herb. Boissier **2**(App. 1)**:** 45 (1894).—*Lecidea parvifolia* Pers. in Gaudichaud, *Voy. Uranie*: 192 (1827); type: Brazil, Rio de Janeiro, Gaudichaud s. n. (PC—holotype, not seen; G 00293379—isotype, image seen).

Phyllopsora weberi L. I. Ferraro, *Bol. Soc. Argent. Bot.* **24:** 179 (1985); type: Argentina, Misiones, Dept. San Ignacio, 08-12-1981, *L. I. Ferraro* et al. 2231 (CTES—holotype, not seen; UPS L-55195!—isotype) (TLC (Brako (1991): no lichen substances. Synonymy according to Brako (1991)).

Description. Elix (2009).

Chemistry. No lichen substances.

Distribution. North, Central and South America, Europe, Africa, Australia, Oceania.

Discussion. The five accessions of *P. parvifolia* cluster together in a strongly supported clade as sister to *P. mediocris* in the ITS tree (Fig. 3). In the mtSSU tree, the specimen from Tanzania groups as sister to a clade consisting of *P. mediocris* and the remaining specimens of *P. parvifolia* and is delimited as a separate species (Fig. 2). In the ITS tree, the accessions are delimited as five separate species (Fig. 3). Also in the ITS tree, the specimen from Tanzania is resolved as sister to the other specimens of *P. parvifolia*, which form a strongly supported clade (Fig. 3). The Tanzanian specimen shows more sequence divergence than the other specimens but is morphologically similar in forming a rosulate thallus with numerous

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phyllidia. Hence, we consider all five specimens belong to the same species for now, although it is possible that the population in Tanzania is genetically isolated from other populations. The European specimen has an overall less developed and smaller thallus than the other specimens, perhaps caused by environmental influences. The sequences of the European specimen, however, do not differ markedly from the others. *Phyllopsora parvifolia* is readily distinguished from other species by its thallus morphology and from its sister *P. mediocris*, which has a squamulose thallus and forms lacinules.

The species is reported here as new to Europe (Portugal, specimen 6365). We have also examined, but not sequenced, a specimen from the Azores: Terceira, Canada do Celis, 15-01-2004, *A. F. Rodrigues* TCCE-46 (B 60-173086).

Phyllopsora parvifoliella (Nyl.) Müll. Arg.

Bull. Soc. Roy. Bot. Belgique **32:** 131 (1893 [1894?]).—*Lecidea parvifoliella* Nyl., *Ann. Sci. Nat., Bot., Sér. 4* **19:** 339 (1863); type: Cuba, s. loc., *C. Wright* s. n., Tuckerman, *Wright Lich. Cub.* No. 182 (BM!—lectotype, designated by Swinscow & Krog (1981): 244; H-NYL 20545!, UPS L-108289!—isolectotypes) (TLC: atranorin, parvifoliellin).

Description. Timdal (2008).

Chemistry. Parvifoliellin (major) and often atranorin (minor to trace).

Distribution. Central and South America, Asia.

Discussion. In this study, we included seven specimens originally identified as *P. parvifoliella* based on the presence of isidia and the detection of parvifoliellin. Surprisingly, they are resolved as two distantly related clades: one clade is left unresolved in a large clade with *P. hispaniolae* and *P. rappiana* among many others (Fig. 4); the other clade is sister to *P. cinchonarum* (Figs 2–4) and described here as the new species *P. concinna* (Fig. 5B). Upon closer examination, we also found several morphological differences, including the isidia and their placement on the squamules: the three specimens from Peru, Indonesia and Thailand agree with the type material of *P. parvifoliella* and form isidia growing from the tip of the squamule lobes, forming an extension of the squamules while the four neotropical specimens of the other clade form cylindrical isidia growing from the squamule surface. We therefore consider the former pantropical clade to represent the true *P. parvifoliella*. See also *P. concinna* for further information.

The three specimens of *P. parvifoliella* are resolved as a supported group in both trees (Figs 2 & 3). mPTP resolves them as representing three separate species due to the long branches (Figs 2 & 3). As they are morphologically congruent, we assume that they comprise one species only. Unfortunately, we could not resolve their closest relatives. Parvifoliellin is a rare compound, known only from *P. concinna*, *P. parvifoliella* and *P. rappiana*; all three also contain atranorin.

The species is new to Asia.

Phyllopsora phaeobyssina (Vain.) Timdal

Biblioth. Lichenol. **106:** 342 (2011).—*Lecidea breviuscula* var. *phaeobyssina* Vain., *Ann. Acad. Sci. Fenn., Ser. A* **6** (7)**:** 127 (1915); type: Guadeloupe, Houelmont, sur un *Coffea arabica*, *P. Duss* 481 (TUR-V 22602!—holotype; NY—isotype, not seen) (TLC: argopsin).

Description. Timdal (2011).

Chemistry. Argopsin (major), norargopsin (absent to minor).

Distribution. Neotropical.

Discussion. In this study, we were able to include only one specimen of *P. phaeobyssina*. The specimen is resolved as a distinct species in both mPTP analyses (Figs 2 & 3) and groups together with *P. teretiuscula* (Figs 2 & 4). The two species are similar in morphology and chemistry but *P. phaeobyssina* forms broader, more flattened squamules and never contains chlorophyllopsorin. See also discussion under *P. teretiuscula*.

Phyllopsora porphyromelaena (Vain.) Zahlbr.

Cat. Lich. Univ. **4**(3)**:** 401 (1926).—*Lecidea porphyromelaena* Vain., *Ann. Acad. Sci. Fenn., Ser. A* **15**(6)**:** 113

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(1921); type: Philippines, Luzon, Bataan Prov., Mount Mariveles, ad truncos arborum, 12-1908, *E. D. Merrill* 6273 (TUR-V 22619!—lectotype, designated by Swinscow & Krog (1981): 224; BM, TUR-V 22620, US—isolectotypes, not seen) (TLC: argopsin (major), norargopsin (major)).

Phyllopsora formosana Zahlbr., *Repert. Spec. Nov. Regni Veg.* **33:** 43 (1933); type: Taiwan, Prov. Taitung, Raisha, 05-01-1926, *Asahina* s. n. (W—lectotype, designated by Swinscow & Krog (1981): 224 (as 'holotype', Art. 9.10), not seen; TNS!—isolectotype) (TLC (Swinscow & Krog 1981): argopsin, norargopsin (as albicans unknowns 1 and 2)).

Descriptions. Timdal & Krog (2001) and Elix (2009), both as *P. albicans*.

Chemistry. Chemotype 1: argopsin (major), norargopsin (major to trace); chemotype 2: argopsin (major), pannarin (major); chemotype 3: unknown compound (major, R_f classes A:4, B′:4–5, C:5), zeorin (major); chemotype 4: argopsin (major), norargopsin (minor to trace), zeorin (minor to rarely trace).

Distribution. Chemotype 1: palaeotropical; chemotype 2: palaeotropical; chemotype 3: Thailand; chemotype 4: neotropical.

Discussion. The species was named *P. albicans* by Swinscow & Krog (1981), Timdal & Krog (2001) and Elix (2006*a*, 2009); the current name *P. porphyromelaena* was established by Timdal (2011) since *P. albicans* is regarded as a synonym of *P. santensis* (Brako 1991). Chemotypes 1 and 2 were recognized by Timdal & Krog (2001), and chemotypes 3 and 4 are recognized in this paper. Brako (1991) treated neotropical material of this species as *P. buettneri* var. *glauca* chemotypes 1 and 3, a distinction of chemotypes that we do not recognize. Hence, here we call those chemotype 4, while var. *glauca* chemotype 2 is treated here as *P. neotinica*.

In total, we include eight accessions of *P. porphyromelaena* in our phylogenetic study: three specimens of chemotype 1, three of chemotype 2, and two of chemotype 3. We had no fresh material of the fourth chemotype for sequencing. The eight accessions are not resolved as a monophyletic clade in either tree (Figs 2–4). In the mtSSU tree, *P. porphyromelaena* chemotypes 1 and 2 cluster weakly together, while those of chemotype 3 cluster with *P. chodatinica* in the ITS tree (Fig. 3). mPTP delimits several different entities corresponding to chemotype and geographical region (Figs 2 & 3). Chemotype 3 might form a separate species but more data are necessary to obtain sufficient phylogenetic support for species description. All accessions form a clade with *P. buettneri* and *P. chodatinica* (Figs 2–4, group B) as well as a larger clade with *P. chlorophaea* and *P. neotinica* (Figs 2 & 4, group B). These species are morphologically similar. *Phyllopsora buettneri* might be confused with *P. porphyromelaena* in particular but forms pruinose and slightly larger lobes than *P. porphyromelaena*. All five species can be distinguished mainly by their differing chemistries (Table 2). The relationships between these species have long been unclear, and the phylogenies show that the currently available molecular data are unable to resolve species delimitations. More in-depth analyses with additional data from all chemical strains of all included species are necessary to understand the limits and relationships of the species involved. See Discussion for further comments.

Phyllopsora pyxinoides (Nyl.) Kistenich *et al.*

Taxon **67:** 894 (2018).—*Crocynia pyxinoides* Nyl., *Sert. Lich. Trop.*: 37 (1891); type: Cuba, 'in ins. Cuba', *C. Wright*, Tuckerman, *Wright Lich. Cub.* Ser. 2, No. 145 (H-NYL 22059—holotype, image seen) (TLC (Harris, on label): atranorin).

Crocynia biatorina (Mont.) Hue, *Mém. Soc. Sci. Nat. Math. Cherbourg* **37:** 231 (1909).—*Parmelia gossypina* var. *biatorina* Mont., *Ann. Sci. Nat., Bot., Sér. 2* **16:** 116 (1841); type: French Guiana, 'ad cortices arborum in insulâ Cayennâ', *Leprieur* 512 (PC—holotype, not seen).

Description. Hue (1909, as *Crocynia biatorina*).

Chemistry. Atranorin (major), stictic acid (major), terpenoids (minor to traces).

Distribution. Pantropical.

Discussion. *Crocynia pyxinoides* was transferred to *Phyllopsora* based on the phylogenetic position of a GenBank accession (*Lücking* 16052) in a molecular tree of the *Ramalinaceae* by Kistenich *et al.* (2018*a*). In

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this study, we include three mtSSU accessions of *P. pyxinoides*, the one from GenBank and two new specimens (Table 1). Here we found that the GenBank accession clustered among our *P. gossypina* specimens and not with the two other *P. pyxinoides* accessions. Therefore the GenBank sequence seems to be a misidentified *P. gossypina* chemotype 2, the norstictic acid strain. The other two accessions grouped into a strongly supported clade and were resolved as a single species in a clade with *P. amazonica*, *P. gossypina*, *P. halei* and *P. imshaugii* (Figs 2 & 4). Longer sequences, as well as sequences of additional specimens (including ITS), might provide better resolution. It seems, however, that *P. gossypina* is not the closest relative of *P. pyxinoides*. This indicates that the former genus *Crocynia* was not monophyletic and corroborates the decision to synonymize it with *Phyllopsora* in Kistenich *et al.* (2018*a*). Sequences of further *Crocynia* species, such as *C. microphyllina*, *C. minutiloba*, *C. mollis* and *C. molliuscula*, are needed to draw further conclusions about the former *Crocynia* species' phylogenetic relationships.

Phyllopsora rappiana (Brako) Elix

Australas. Lichenol. **58:** 6 (2006).—*Phyllopsora corallina* var. *rappiana* Brako, *Fl. Neotrop. Monogr.* **55:** 42 (1991); type: USA, Florida, Sarasota Co., Myakka River State Park, along Myakka River, moist and shady oak wood and scrub, 16-08-1985, *L. Brako* 8229 (NY!—holotype) (TLC: atranorin, parvifoliellin).

Descriptions. Brako (1991), Elix (2009).

Chemistry. Parvifoliellin (major), atranorin (major).

Distribution. North, Central and South America, Australia.

Discussion. The two accessions of *P. rappiana* cluster together in a supported clade (Figs 2 & 3). mPTP resolves them as separate species in both analyses due to the long branches (Figs 2 & 3). Based on morphology and chemistry, we still regard them as one species. In the mtSSU tree they are resolved as sister, among others, to *P. glaucella* (Fig. 2) from which they differ in morphology and chemistry. The species may be confused with *P. parvifoliella* and *P. concinna* because of the presence of isidia, parvifoliellin and atranorin (the latter compound not always present). The phylogenies show, however, that the species are not closely related and that the occurrence of the rare lichen substance parvifoliellin has evolved independently in those species (Figs 2–4). *Phyllopsora rappiana* has a more reduced thallus and shorter, thinner isidia than *P. parvifoliella* and *P. concinna*, and generally a higher concentration of atranorin.

Phyllopsora rosei Coppins & P. James

Lichenologist **11:** 166 (1979); type: UK, Wales, Merioneth, Dolgellau, vallis Nant Gwynant, in cortice umbroso *Fraxini*, cum *Catillaria pulverea*, alt. *c.* 30 m, 04-1960, *P. W. James* (BM—holotype, not seen).

Description. Coppins & James (1979), Rose *et al.* (2009).

Chemistry. Argopsin (major), norargopsin (minor or absent).

Distribution. Europe.

Discussion. In this study, we include four specimens of *P. rosei*, two from France and two from the UK. We found our accessions to form a well-supported clade together with accessions of *P. hispaniolae* in the mtSSU tree (Fig. 2), while they are nested in *P. hispaniolae* in the ITS tree (Fig. 3). Both mPTP analyses resolve *P. rosei* and *P. hispaniolae* to form one species only. We were surprised by these results as the species are morphologically and chemically different: *P. rosei* forms a minutely granulose thallus on a white prothallus, thinly 1–3-septate ascospores, and contains argopsin and often norargopsin, while *P. hispaniolae* forms deeply divided, coralloid squamules on a reddish brown prothallus, simple ascospores and contains argopsin and chlorophyllopsorin. Hence, we suggest keeping the two species separate until further specimens are examined.

Phyllopsora santensis (Tuck.) Swinscow & Krog

Lichenologist **13:** 236 (1981).—*Lecidea santensis* Tuck., *Amer. J. Sci. Arts, Ser. 2* **25:** 428 (1858); type: USA,

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South Carolina, Santee Canal, 1849, *H. W. Ravenel* 182 (FH-TUCK 2822—lectotype, designated by Swinscow & Krog (1981): 236 (as 'holotype', Art. 9.10), not seen; B 35832!, BG L-4032!, O L-150045!—isolectotypes, issued as *Reliq. Tuck.* No. 15) (TLC: argopsin, norargopsin).

Phyllopsora albicans Müll. Arg., *Bull. Soc. Roy. Bot. Belgique* **32:** 132 (1893 [1894?]); type: Costa Rica, Terraba, Tonduz, 1893, ex hb. Müll. Arg. (G 110889!—holotype; US—isotypes, not seen) (TLC: argopsin, norargopsin).

Lecidea miradorensis Vain., *Dansk Bot. Ark.* **4**(11)**:** 22 (1926).—*Phyllopsora miradorensis* (Vain.) Gotth. Schneid., *Biblioth. Lichenol.* **13:** (1980), nom. inval., Art. 36.1 (a); type: Mexico, Veracruz, ad Mirador, 18-03-1842, *Liebmann* 7373 (TUR-V 34034—lectotype, designated by Swinscow & Krog (1981): 236, not seen; FH, TUR-V 34035—isolectotypes, not seen) (TLC: (Swinscow & Krog 1981): argopsin, norargopsin (as albicans unknowns 1 and 2). Synonymy according to Brako (1989, 1991)).

Descriptions. Timdal (2008), Elix (2009).

Chemistry. Argopsin (major), norargopsin (submajor to minor).

Distribution. North, Central and South America, Asia, Australia.

Discussion. The three accessions of *P. santensis* form a strongly supported cluster in an otherwise unresolved clade (Figs 2 & 3). They are delimited as one entity in both mPTP analyses (Figs 2 & 3). The species resembles *P. phaeobyssina* morphologically and chemically but differs, for example, in forming longer ascospores. Both species cluster in the same higher clade in the trees (Figs 2–4), indicating that a relationship is possible.

Phyllopsora subhispidula (Nyl.) Kalb & Elix

Biblioth. Lichenol. **57:** 293 (1995).—*Psoroma subhispidulum* Nyl., *Ann. Sci. Nat., Bot., Sér. 4* **11:** 256 (1859); type: La Réunion, 'Ins. Borbonia', *Lepervanche–Mézières* 73 (H-NYL 30812!—holotype) (TLC (Kalb & Elix 1995): argopsin, norargopsin, zeorin).

Description. Timdal & Krog (2001).

Chemistry. Argopsin (major), norargopsin (minor), zeorin (major), atranorin (trace).

Distribution. Africa, Asia.

Discussion. The three accessions of *P. subhispidula* group together in a supported clade in the phylogenies and are resolved as one species in both mPTP analyses (Figs 2 & 3). It is weakly resolved as sister to the *hispaniolae-nemoralis-rosei* clade (Figs 3 & 4), from which it differs greatly in morphology.

Phyllopsora subhispidula is morphologically highly similar to *P. buettneri* but differs in forming long, cylindrical isidia, not phyllidia. Chemically, it conforms to *P. buettneri* chemotype 4 (argopsin, norargopsin and zeorin) which we have not seen nor sequenced. Kalb & Elix (1995) erroneously synonymized Brako's *P. buettneri* var. *glauca* with *P. subhispidula*, which reflects the morphological similarity between the two species. Indeed, *P. subhispidula* is found in the same larger clade in the trees as *P. melanoglauca* (Figs 2–4), the former chemotype 3 of *P. buettneri*, indicating a possible relationship.

Phyllopsora swinscowii Timdal & Krog

Mycotaxon **77:** 88 (2001); type: Mauritius, Black River, along the path from Plaine Champagne towards Piton de la Petite Rivière Noire, 20°25′S, 57°25′E, 600 m alt., 05-11-1991, *Krog & Timdal* MAU9/50 (O L-21220!—holotype) (TLC: methyl 2,7-dichloropsoromate, methyl 2,7-dichloronorpsoromate; DNA: MK352143 (mtSSU)).

Descriptions. Timdal & Krog (2001), Timdal (2008), Elix (2009).

Chemistry. Methyl 2,7-dichloronorpsoromate (major), methyl 2,7-dichloropsoromate (major to minor).

Distribution. Central and South America, Africa. Asian and Australian records need confirmation.

Discussion. The five accessions of *P. swinscowii*, including the holotype, form a well-supported clade (Figs 2 & 3) and are sister to *P. africana* (Figs 2–4). The two species also form a complex with *P. ochroxantha* (Figs 2 & 3, group C). The ITS mPTP analysis resolves all specimens of *P. swinscowii* as belonging to a single entity (Fig. 3), while the mtSSU mPTP analysis suggests a single species for all accessions of *P. swinscowii* and *P. africana* (Fig. 2).

The three species in clade C are morphologically nearly identical. *Phyllopsora swinscowii* differs from *P. ochroxantha* in its chemistry (methyl 2,7-dichloropsoromate and methyl 2,7-dichloronorpsoromate in *P. swinscowii* vs.

chlorophyllopsorin and phyllopsorin in *P. ochroxantha*). The delimitation from *P. africana*, on the other hand, is more difficult. Chemotype 2 of *P. africana* is identical to the chemistry of *P. swinscowii*, but chemotypes 1 and 3 differ in containing chlorophyllopsorin. As *P. swinscowii* is morphologically and chemically identical to *P. africana* chemotype 2, they should be regarded as a cryptic taxon pair. However, it is questionable whether *P. swinscowii* and *P. africana* should be synonymized (see discussion under *P. africana* and the general Discussion) and we suggest investigating this complex with additional material before making a conclusion.

Phyllopsora teretiuscula Timdal

Biblioth. Lichenol. **106:** 346 (2011); type: Cuba, Pinar del Río, Reserva de la Biosfera Sierra del Rosario, N of and near lake 'La Palma', near river, downstream from the path/road, 22°51·31′N, 82°56·25′W, 140–145 m alt., over mosses on trunk of *Roystonea regia* in mixed hardwood forest, 21-03-2007, *T. Tønsberg* 37814 (BG L-87831!—holotype) (TLC: argopsin, norargopsin; DNA: MK352152 (mtSSU), MK352327 (ITS)).

Description. Timdal (2011).

Chemistry. Argopsin (major), norargopsin (minor to absent), chlorophyllopsorin (minor to absent).

Distribution. The West Indies.

Discussion. In our study we use three accessions of *P. teretiuscula*, including the holotype. In both trees, all three accessions form a well-supported clade and are delimited as one species by mPTP (Figs 2 & 3). *Phyllopsora teretiuscula* is resolved as sister to *P. phaeobyssina* (Figs 2 & 4). The two species are morphologically and chemically quite similar. *Phyllopsora teretiuscula* differs, however, in forming narrower, more terete lobes and in sometimes containing chlorophyllopsorin, while *P. phaeobyssina* forms broader lobes and never contains chlorophyllopsorin. More specimens of *P. phaeobyssina* and sequences of additional genetic markers of both species are necessary to investigate their possible synonymy.

The species is new to Costa Rica and Puerto Rico.

Phyllopsora thaleriza (Stirt.) Swinscow & Krog

Lichenologist **13:** 238 (1981).—*Lecidea thaleriza* Stirt., *Rep. Trans. Glasgow Soc. Fld Nat.* **5:** 217 (1877); type: South Africa, Eastern Cape, Somerset East, Boschberg, 1874, *McOwan* (BM—holotype, not seen) (TLC (Swinscow & Krog 1981): atranorin, trace).

Psora compaginata Müll. Arg., *Rev. Mycol.* (*Toulouse*) **10:** 60 (1888).—*Phyllopsora compaginata* (Müll. Arg.) Swinscow & Krog, *Lichenologist* **13:** 240 (1981); type: Paraguay, Cerro San Thomas, 06-1881, *Balansa* 4134 (G 00292483—holotype, image seen) (synonymy according to Brako (1989)).

Description. Swinscow & Krog (1981).

Chemistry. Atranorin (minor to trace).

Distribution. South America, Africa.

Discussion. Swinscow & Krog (1981) considered *P. thaleriza* to be intermediate between a *Phyllopsora* and a *Bacidia* because of its nearly crustose thallus as well as dense white prothallus. Brako (1989) excluded the species from *Phyllopsora* because of differences in the hypothecium, thallus structure and algal symbiont. Kistenich *et al.* (2018*a*) resolved it to cluster, unrelated to *Bacidia*, among other *Phyllopsora* species in a molecular phylogeny of the family. Here we corroborate these results: all four accessions of *P. thaleriza* form a strongly supported clade in both phylogenetic trees and both mPTP analyses delimit them as one species (Figs 2 & 3). Due to poor resolution of the trees, we could not identify their closest relative. The species is readily distinguished by its areolate-crustose thallus, lack of vegetative dispersal units and the presence of atranorin.

B. Poorly understood, doubtful and fossil species

Phyllopsora bibula (Taylor) Swinscow & Krog

Lichenologist **13:** 239 (1981).—*Lecanora bibula* Taylor, *London J. Bot.* **6:** 160 (1847); type: Chile, ins. Juan Fernandez, in cortice arbor., locis umbrosis, 04-1830, *Bertero* 1648 (FH—lectotype, designated by Brako (1991): 29 (as 'holotype', Art. 9.10), not seen; BM!, H-NYL 20540!, H-NYL PM4109!—isolectotypes) (TLC (Swinscow & Krog 1981): fatty acid).

This poorly understood species is known only from the type collection. No attempt was

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made to extract DNA from the examined isotypes, which are in poor condition. Zahlbruckner (1921–1940) lists this species as a synonym of *P. parvifolia* which, however, generally forms larger squamules. Further collections of similar specimens from the type locality are necessary to gain more knowledge regarding the correct taxonomic affiliation of *P. bibula*.

Phyllopsora catervisorediata G. K. Mishra *et al.*

Mycotaxon **115:** 33 (2011); type: India, Uttarakhand, Bageshwar Distr., en route to Pindari glacier, from Dwali to Khati, 2734–3210 m alt., on bark, 13-05-2007, *S. Joshi & Y. Joshi* 07-008932 (LWG—holotype, not seen) (TLC (Mishra *et al.* 2011): atranorin).

This species is known only from the type material. It was not studied by us due to the lack of response from LWG to our repeated loan requests. The presence of soredia indicates that it might not belong in *Phyllopsora*, as does the statement in the protologue that it is close to *P. soralifera*, a species that is excluded from the genus here. Sequences are needed to understand the correct taxonomic affiliation of this species.

Phyllopsora cinerella Zahlbr.

Ark. Bot. **31A**(6)**:** 18 (1944); type: USA, Hawaii, Iles Sandwich, Robinson Summer House Kauai, 02-1910, *Faurie* 308 (PC—lectotype, designated by Brako (1991): 40, not seen), *Faurie* 307 (BM!—syntype) (TLC (Brako 1991): phyllopsorin, chlorophyllopsorin).

Although treated as a synonym of *P. ochroxantha* by Brako (1991), we found the isotype in BM indeterminable.

Phyllopsora densiflorae (Vain.) Swinscow & Krog

Lichenologist **13:** 241 (1981).—*Lecidea densiflorae* Vain., *Bot. Mag.* (*Tokyo*) **35:** 67 (1921); type: Japan, Prov. Kozuke, on *Pinus densiflora*, 25-02-1918, *A. Yasuda* 350 (TUR-V 22632!—holotype) (TLC: unidentified fatty acid in R_f class B:6).

This poorly understood species is known only from the type collection and no attempt was made to extract DNA from it. According to Brako (1991), it is a synonym of *P. corallina*, while Swinscow & Krog (1981) considered a possible synonymy with *P. confusa*. We regard *P. densiflorae* as being crustose, consisting of areoles up to 0·2 mm diam., and not synonymous with either of the other two. Rather it should be considered for inclusion in *Biatora*. Whereas Swinscow & Krog (1981) and Brako (1991) reported no lichen substances from the holotype, our TLC examination of the specimen revealed an unidentified fatty acid. The extent of morphological variation in this species cannot be assessed without further specimens and thus DNA sequences will have to be obtained to determine its status.

Phyllopsora dominicana Rikkinen

J. Exp. Bot. **59:** 1008 (2008); type: *Poinar* B 1–23 (Oregon State University—holotype, not seen).

This species is known only as a fossil from Dominican amber.

Phyllopsora griseocastanea (Vain.) Swinscow & Krog

Lichenologist **13:** 241 (1981).—*Lecidea griseocastananea* Vain., *Ann. Acad. Sci. Fenn., Ser. A* **15**(6)**:** 114 (1921); type: Philippines, Luzon, Benguet Prov., Pauai, ad corticem arboris, 1909, *E. D. Merrill* 6651 (TUR-V 22625!—holotype) (TLC: no lichen substances).

This poorly understood species is known only from the type collection and no attempt was made to extract DNA from it. Swinscow & Krog (1981) mention a similarity with *P. manipurensis* in the coloration of the hypothecium, but DNA sequence data are necessary to investigate the taxonomic affinity of the type.

Phyllopsora magna Kaasalainen *et al.*

Earth Environm. Sci. Trans. Roy. Soc. Edinburgh **107:** 322 (2017); type: AMNH DR-15-3 (American Museum of Natural History, New York—holotype, not seen).

This species is known only as a fossil from Dominican amber.

Phyllopsora manipurensis (Müll. Arg.) Müll. Arg.

Bull. Soc. Roy. Bot. Belgique **32:** 132 (1893 [1894?]).—*Psora manipurensis* Müll. Arg., *J. Linn. Soc., Bot.* **29:** 219 (1893); type: India, Manipoor, *G. Watt* (G—holotype, image seen; BM—isotype, not seen) (TLC (Swinscow & Krog 1981): atranorin, trace).

The species is known only from the type material. Mishra *et al.* (2011) suggest a close

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relationship to *P. subcrustacea*, another poorly known species. Sequence data might clarify its taxonomic affiliation.

Phyllopsora microphyllina (Nyl.) Swinscow & Krog

Lichenologist **13:** 243 (1981).—*Lecidea microphyllina* Nyl., *Ann. Sci. Nat., Bot., Sér. 4* **19:** 347 (1863); type: Cuba, s. loc., *C. Wright* s. n. (H-NYL 17345a!—holotype; BM!, UPS L-135785!—isotypes, issued as Tuckerman, *Wright Lich. Cub*. No. 211) (TLC: no lichen substances).

We know of no reliably identified, recently collected material of this poorly understood species and have not attempted DNA extraction of the old type material. It is characterized by having a squamulose thallus without vegetative dispersal units, acicular ascospores, and by the lack of lichen substances. It is morphologically similar to *P. neofoliata* but differs in chemistry and ascospore size. Due to the acicular ascospores, it is doubtful whether this species really belongs in *Phyllopsora*. It is possible that it should be excluded like many other former *Phyllopsora* species having acicular ascospores, such as *Bacidina lacerata* or *Parallopsora leucophyllina*.

Phyllopsora microsperma Müll. Arg.

Bull. Herb. Boissier **2:** 89 (1894); type: Mexico, Jalisco, 1890, *J. W. Eckfeldt* 190 (G 00293373—holotype, image seen) (TLC (Swinscow & Krog 1981): traces of atranorin(?) and triterpenoid).

Lecidea subglabella Malme, *Ark. Bot.* **28A**(7): 41 (1936).—*Phyllopsora subglabella* (Malme) Swinscow & Krog, *Lichenologist* **13:** 245 (1981); type: Brazil, Mato Grosso, Guia pr. Cuyabá, in silva ripæ fluvii, 14-05-1894, *G. O. A. Malme, Lich. Regnell.* 2547 (S!—lectotype, designated by Brako (1991): 48 (as 'holotype', Art. 9.10); UPS L-10379!—isolectotype) (TLC (Brako 1991): no lichen substances. Synonymy according to Brako (1991)).

Lecidea glabella Nyl., *Sert. Lich. Trop.*: 37 (1891), nom. illeg. (non Kremp. 1876).—*Phyllopsora glabella* Swinscow & Krog, *Lichenologist* **13:** 241 (1981); type: Cuba, s. loc., ad palmas, *C. Wright* s. n., Tuckerman, *Wright Lich. Cub*. Ser. 2, 142 (H-NYL 20518!— holotype) (TLC (Brako 1991): no lichen substances. Synonymy according to Brako (1991)).

We know only a small number of collections of this species and all were made before the 1960s. As we have been able to generate sequences of specimens from the late 1960s, it might be possible to generate sequences from the Haitian specimen of *P. microsperma* collected in 1958, when taking special measures to avoid contamination. However, we decided not to attempt DNA extraction from those specimens, anticipating that better methods for extracting and sequencing old material will be developed. The species is characterized by adnate, rather thick, shiny squamules growing on a reddish brown prothallus, short ellipsoid ascospores as well as a lack of vegetative dispersal units and lichen substances. It may be similar to *P. breviuscula* and *P. mauritiana* but both species form larger ascospores.

Phyllopsora minor Brako

Mycotaxon **35:** 15 (1989).—*Lecidea corallina* var. *schizophylloides* Vain., *J. Bot.* **34:** 106 (1896); type: St. Vincent and the Grenadines, St. Vincent, Richmont Peak, ad corticem arboris, 1000–2000 ft alt., *W. R. Elliot* 261[a] (TUR-V 22612!—lectotype, designated by Swinscow & Krog (1981): 240; BM!—isolectotype) (TLC: no lichen substances).

Phyllopsora minor is known only from the old type material and we have not attempted to extract DNA. The species is generally characterized by an effuse thallus consisting of irregularly oriented, narrow squamules which are closely adnate to well developed, growing on a reddish brown prothallus, medium to dark brown apothecia with ellipsoid ascospores, and the lack of lichen substances. Sequences are necessary to determine the phylogenetic placement of this species.

Phyllopsora purpurescens (Vain.) Zahlbr.

Cat. Lich. Univ. **4**(3)**:** 401 (1926).—*Lecidea purpurescens* Vain., *Univ. Calif. Publ. Bot.* **12:** 10 (1924); type: Tahiti, in valle Punaruu, *W. A. Setchell & H. E. Parks* 5380 p.p. (TUR-V 22618—holotype, not seen; BM 001048828, US 00433394—isotypes, images seen).

The species is known only from the old type collection and we did not attempt to extract DNA. Swinscow & Krog (1981) found the species to be morphologically similar to *P. societatis* and to contain the same fatty acids; the two species are only distinguished by the colour of their prothallus. Sequence data should be obtained from both species to investigate their potential synonymy and their phylogenetic placement in *Phyllopsora*.

Phyllopsora societatis (Vain.) Zahlbr.

Cat. Lich. Univ. **4**(3)**:** 401 (1926).—*Lecidea societatis* Vain., *Univ. Calif. Publ. Bot.* **12:** 10 (1924); type: Tahiti, Papehue River, 07-06-1922, *W. A. Setchell & H. E. Parks* 5349 (TUR-V 22614!—holotype; BM—isotypes, not seen) (TLC: no lichen substances).

The species is known only from the old type collection and we did not attempt to extract DNA. It might be conspecific with *P. purpurescens* (Swinscow & Krog 1981); see discussion under that species. We did not detect the fatty acids in the holotype that were reported from the isotype in BM by Swinscow & Krog (1981).

Phyllopsora subcrustacea (Malme) Brako

Mycotaxon **35:** 15 (1989).—*Lecidea corallina* var. *subcrustacea* Malme, *Ark. Bot.* **28A**(7)**:** 47 (1936); type: Paraguay, Asuncion, 18-08-1893, *G. O. A. Malme* Lich. Regnell. 1612B (S!—lectotype, designated by Brako (1991): 57 (as 'holotype', Art. 9.10); UPS L-010380!—isolectotype, not seen) (TLC (Brako 1991): no lichen substances).

Phyllopsora subscrustacea is another species known only from the type collection. We were not able to locate any reliably identified, recently collected material from the geographical region where this poorly understood species was described (Paraguay), and did not extract DNA from the old type material. The species is characterized by closely adjoined, adnate to ascending squamules, which form an almost continuous crust, cylindrical isidia and bright orange-red, marginate apothecia. The species might be similar to *P. loekoesii* but sequences of the type material are essential for determining its correct phylogenetic position.

Phyllopsora subhyalina (Stirt.) Zahlbr.

Cat. Lich. Univ. **4**(3)**:** 401 (1926).—*Lecidea subhyalina* Stirt., *Trans. & Proc. Roy. Soc. Victoria* **17:** 77 (1881); type: Australia, Victoria, Gippsland, Waterloo, *Stirton* 8662 (BM—holotype, not seen).

The type material was studied by Swinscow & Krog (1981) and Brako (1991) but left uninterpreted due to its poor condition. Swinscow & Krog (1981) noticed the absence of a prothallus and Brako (1991) noted the gelatinized apothecia, characters that are not typical of *Phyllopsora* species. It is therefore unclear whether the species belongs in *Phyllopsora* and sequence data are necessary for clarification.

Lecidea thysaniza Nyl.

Lich. Nov. Zel.: 82 (1888); type: 'Nova Zelandia', 1867, *Knight* 117 (H-NYL 20481!—holotype) (TLC: terpenoids).

The species is known only from the old type collection and we did not attempt DNA extraction. The type material might represent a *Phyllopsora* species based on its thallus morphology but sequences are necessary for clarification.

Phyllopsora viridis Paulson

J. Siam Soc., Nat. Hist. Suppl. **2:** 101 (1930); type: Thailand, Kaw Tao, *c.* 100 m alt., 22-09-1918, *Paulson* 29 (BM—holotype, not seen).

This species is known from the type collection only. The type material was studied by Swinscow & Krog (1981) and Brako (1991); the former found no *Phyllopsora* in the collection and the latter found the material too small for comprehensive examination.

C. Excluded species

Phyllopsora aleuroides (Stirt.) Müll. Arg.

Bull. Herb. Boissier **2**(App. 1)**:** 45 (1894).—*Lecidea aleuroides* Stirt., *J. Linn. Soc., Bot.* **14:** 469 (1875); type: not seen (see Galloway & James 1985).

This species belongs in *Psoromidium* Stirton (Galloway & James 1985; Brako 1989; Jørgensen & Andersen 2015).

Phyllopsora atrocarpa Timdal

Lichenologist **40:** 341 (2008); type: Peru, Loreto, Jenaro Herrera, within a 3·6 km distance from the Research Centre, N of the road, site 116, 4°53·87′S, 73°38·85′W, 120–150 m alt., tree trunk in rainforest, 28-09-2006, *E. Timdal* 10425 (O L-144795!—holotype) (TLC: fumarprotocetraric acid, 2'-O-methylhyperlatolic acid).

This species probably belongs to an undescribed genus in the family *Malmideaceae*, together with *P. lividocarpa* and *P. nigrocincta* (Kistenich *et al.* 2018*a*).

Phyllopsora borbonica Timdal & Krog

Mycotaxon **77:** 68 (2001); type: La Réunion, along road towards Plaine d'Affoches, above Bras Citron, at point where road meets track, 20°57′S, 55°25′E, 1220 m alt., 1996, *H. Krog & E. Timdal* RE8/12 (O L-797!—holotype) (TLC: no lichen substances).

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Kistenich *et al.* (2018*a*) showed that this species belongs in the resurrected genus *Sporacestra*.

Phyllopsora brakoae Timdal

Lichenologist **40:** 343 (2008); type: Peru, Loreto, Reserva Nacional Allpahuayo Mishana, within a 2·3 km distance from Centro de Investigaciones Allpahuayo, N of the road, site 43, 3°58·48′S, 73°25·86′W, 120–150 m alt., tree trunk in rainforest, "bosque de varillal seco", 22-09-2006, *E. Timdal* 10253 (O L-144623!—holotype) (TLC: no lichen substances).

Kistenich *et al.* (2018*a*) transferred this species to the new genus *Parallopsora* based on DNA sequence data.

Phyllopsora cognata (Nyl.) Timdal

Biblioth. Lichenol. **106:** 331 (2011).—*Lecidea cognata* Nyl., *Ann. Sci. Nat., Bot., Sér. 4* **19:** 347 (1863); type: Cuba, s. loc., *C. Wright*, Tuckerman, *Wright Lich. Cub.* 218 (BM!—lectotype, designated by Timdal (2011): 331; UPS L-135790!—isolectotype) (TLC: atranorin).

Unpublished sequences of this species have shown that it does not belong in *Phyllopsora*.

Phyllopsora congregans (Zahlbr.) D. J. Galloway

New Zealand J. Bot. **21:** 196 (1983).—*Lecidea congregans* Zahlbr., *Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Kl.* **104:** 305 (1941); type: not seen (see Brako 1989).

This species belongs in *Trapeliopsis* Hertel & Gotth. Schneid. (Brako 1989).

Phyllopsora conwayensis Elix

Australas. Lichenol. **59:** 24 (2006); type: Australia, Queensland, Conway State Forest, 18 km E of Prosperpine, 20°21′S, 148°45′E, 180 m alt., in lowland rainforest, on tree trunk, *J. A. Elix & H. Streimann* 20190 (BRI—holotype, fragment seen; B 125907!—isotype).

Unpublished sequences of the isotype have shown that the species does not belong in *Phyllopsora*.

Phyllopsora coroniformis (Kremp.) Zahlbr. in Engler

Nat. Pflanzenfam. **1, 1***(225)**:** 138 (1906).—*Lecidea coroniformis* Kremp., *Verh. K. K. Zool.-Bot. Ges. Wien.* **18:** 326 (1868); type: USA, Texas, s. loc., s. coll., ex hb. Krempelhuber October 1883 (M!—holotype) (TLC: norstictic acid).

This species belongs in *Psora* Hoffm. and is a synonym of *Psora crenata* (Taylor) Reinke (Timdal 1986).

Phyllopsora cryptocarpa Riddle

Mycologia **15:** 80 (1923); type: not seen (see Brako 1989).

This species belongs in *Fellhanera* Vězda (Brako 1989).

Phyllopsora curatellae (Malme) Swinscow & Krog

Lichenologist **13:** 240 (1981).—*Lecidea curatellae* Malme, *Ark. Bot.* **28A**(7)**:** 42 (1936); type: Brazil, Mato Grosso, Cuyabá, in "cerrado", 27-11-1893, *G. A. O. Malme* 2038 (S!—lectotype, designated by Swinscow & Krog (1981): 240).

According to Brako (1989, 1991), this species belongs in an undescribed genus in the *Lecanoraceae* Körb.

Phyllopsora glaucescens Timdal

Lichenologist **40:** 349 (2008); type: Peru, Loreto, Jenaro Herrera, within a 3·6 km distance from the Research Center, N of the road, site 111, 4°53·88′S, 73°38·90′W, 120–150 m alt., tree trunk in rainforest, 28-09-2006, *E. Timdal* 10418 (O L-144788!—holotype) (TLC: methyl barbatate).

Unpublished sequences of several specimens, including the holotype, have shown that this species does not belong in *Phyllopsora*.

Phyllopsora labriformis Timdal

Lichenologist **40:** 350 (2008); type: Peru, Loreto, Jenaro Herrera, within a 3·6 km distance from the Research Center, N of the road, site 112, 4°53·93′S, 73°83·91′W, 120–150 m alt., tree trunk in rainforest, 28-09-2006, *E. Timdal* 10419 (O L-144789!—holotype) (TLC: methyl barbatate).

Kistenich *et al.* (2018*a*) placed this species in the new genus *Parallopsora* based on DNA sequence data.

Phyllopsora lacerata Timdal

Lichenologist **40:** 352 (2008); type: Peru, Loreto, Reserva Nacional Allpahuayo Mishana, within a 2·3 km distance from Centro de Investigaciones Allpahuayo, N of the road, site 19, 3°57·31′S, 73°25·46′W, 120–150 m alt., tree trunk in rainforest, 21-09-2006, *E. Timdal* 10213 (O L-144583!—holotype) (TLC: no lichen substances).

This species was shown to belong to *Bacidina* (Kistenich *et al.* 2018*a*).

Phyllopsora leucophyllina (Nyl.) Timdal

Lichenologist **40:** 352 (2008).—*Lecidea leucophyllina* Nyl., *Ann. Sci. Nat., Bot., Sér. 4* **19:** 347 (1863); type: Cuba, 'in ins. Cuba', *C. Wright* s. n. (H-NYL 17345e!—lectotype, designated here, MycoBank typification MBT 387680;

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BM!, H-NYL 17345c!, UPS L-108156!—isolectotypes) (TLC: homosekikaic acid, sekikaic acid).

The new genus *Parallopsora* was established to accommodate this species based on DNA sequence data (Kistenich *et al.* 2018*a*).

Phyllopsora lividocarpa Timdal

Lichenologist **40:** 353 (2008); type: Peru, Loreto, Jenaro Herrera, within a 3·6 km distance from the Research Center, N of the road, site 126, 4°53·66′S, 73°38·56′W, 120–150 m alt., tree trunk in rainforest, 30-09-2006, *E. Timdal* 10447 (O L-144817!—holotype) (TLC: 2'-O-methylhyperlatolic, an unknown fatty acid).

This species probably belongs to an undescribed genus in the family *Malmideaceae*, together with *P. atrocarpa* and *P. nigrocincta* (Kistenich *et al.* 2018*a*).

Phyllopsora longispora Swinscow & Krog

Nordic J. Bot. **5:** 493 (1985); type: Kenya, Western Province, Kakamega District, Kakamega Forest, near Forest Station (*c.* 13 km ESE of Kakamega). Alt. *c.* 1700 m, 0°15′N, 34°52′E, on the trunk of a tree in dense rainforest, 20-01-1970, *R. Santesson* 21698a (UPS—holotype!) (TLC (Swinscow & Krog 1985): small amounts of triterpenoids).

We have unpublished sequences of this species which suggest a close relationship to the genus *Aciculopsora* Aptroot & Trest (*Ramalinaceae*).

Phyllopsora melanocarpa Müll. Arg.

Hedwigia **34:** 28 (1895); type: not seen (see Brako 1989).

This species belongs in *Neophyllis* F. Wilson and is a synonym of *N. pachyphylla* (Müll. Arg.) Gotth. Schneid. (Swinscow & Krog 1981; Brako 1989).

Phyllopsora nigrocincta Timdal

Lichenologist **40:** 354 (2008); type: Peru, Loreto, Jenaro Herrera, within a 3·6 km distance from the Research Center, N of the road, site 124, 4°53·44′S, 73°37·39′W, 120–150 m alt., tree trunk in rainforest, 29-09-2006, *E. Timdal* 10443 (O L-144813!—holotype) (TLC: fumarprotocetraric acid, norsolorininc acid).

This species probably belongs to an undescribed genus in the family *Malmideaceae*, together with *P. atrocarpa* and *P. lividocarpa* (Kistenich *et al.* 2018*a*).

Phyllopsora pertexta (Nyl.) Swinscow & Krog

Lichenologist **13:** 244 (1981).—*Lecidea pertexta* Nyl., *Ann. Sci. Nat., Bot., Sér. 4* **19:** 347 (1863); type: Cuba, 'in ins. Cuba', *C. Wright* s. n. (H-NYL 17344, left specimen!—lectotype, designated here, MycoBank typification MBT 387681) (TLC: no lichen substances).

The genus *Sporacestra* has been resurrected to accommodate this species (Kistenich *et al.* 2018*a*).

Phyllopsora pocsii Vězda

Lich. Rar. Exsicc. **49:** 2 (2003); type: Tanzania, montes Kiboriani, prope Mpwapwa, ad latera montis prope Kikombo, 1200 m alt., ad corticem arborum, 11-05-1972, *T. Pócs & L. Mezösi* 6564/C, Vězda, *Lich. Rar. Exsicc.* No 484 (BM!, GZU!—isotypes) (TLC: no lichen substances).

Our unpublished sequences of the isotype in GZU have shown that the species does not belong in *Phyllopsora*.

Phyllopsora pyrrhomelaena (Tuck.) Swinscow & Krog

Lichenologist **13:** 244 (1981).—*Biatora pyrrhomelaena* Tuck., *Amer. J. Sci. Arts, Ser. 2* **28:** 205 (1859); type: Cuba, Monte Verde Woods, on trunks of trees near the ground, *C. Wright* s. n., Tuckerman, *Wright Lich. Cub.* No. 178 (FH 286104!—lectotype, designated here, MycoBank typification MBT 387682; FH 197468!, UPS L-74560!—isolectotypes) (TLC: norsolorinic acid and at least three additional pink pigments).

This species is morphologically and chemically similar to *P. atrocarpa*, *P. lividocarpa* and *P. nigrocincta*. Kistenich *et al.* (2018*a*) have shown that the three latter species belong to an unknown genus in the family *Malmideaceae*.

Phyllopsora soralifera Timdal

Lichenologist **40:** 358 (2008); type: Peru, Loreto, Reserva Nacional Allpahuayo Mishana, within a 2·3 km distance from Centro de Investigaciones Allpahuayo, N of the road, site 78, 3°57·80′S, 73°25·59′W, 120–150 m alt., tree trunk in rainforest, 24-09-2006, *E. Timdal* 10342 (O L-144712!—holotype) (TLC: no lichen substances).

Unpublished sequences of several specimens have shown that the species does not belong in *Phyllopsora*.

Phyllopsora sorediata (Aptroot & Sparrius) Timdal

Lichenologist **39:** 341 (2008).—*Triclinum sorediatum* Aptroot & Sparrius in Aptroot *et al.*, *Fungal Diversity* **24:**

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130 (2007); type: Thailand, Uthai Thani Prov., Huay Kha Khaeng Wildlife Sanctuary, Kapou Kapiang, 15°29′N, 99°18′E, 500 m alt., on bark, 14-02-1993, *B. Aguirre-Hudson, P. W. James & P. A. Wolseley* 2817 (BM—holotype, not seen; ABL—isotype, not seen).

Kistenich *et al.* (2018*a*) have shown that this species belongs in *Bacidia*.

Phyllopsora stylophora (Malme) Swinscow & Krog

Lichenologist **13:** 245 (1981).—*Lecidea stylophora* Malme, *Ark. Bot.* **28A**(7)**:** 40 (1936); type: Brazil, Mato Grosso, Serra da Chapada, Buriti, in silvula, 27-06-1894, *G. A. O. Malme* s. n. (S!—lectotype, designated by Brako (1991): 58 (as 'holotype', Art. 9.10); G 00293002—isolectotype, image seen; H, US—isolectotypes, not seen) (TLC (Brako 1991): atranorin, terpenoids).

According to Brako (1989, 1991), this species belongs in an undescribed genus in the *Lecanoraceae*.

Phyllopsora subcorallina Zahlbr.

Ann. Mycol. **33:** 43 (1935); type: not seen (see Brako 1989).

This species belongs in *Catinaria* Vain. (Brako 1989).

Phyllopsora subfilamentosa Zahlbr.

Ann. Mycol. **33:** 44 (1935); type: not seen (see Brako 1989).

This species belongs in *Fuscidea* V. Wirth & Vězda (Brako 1989).

Phyllopsora tobagensis Timdal

Biblioth. Lichenol. **106:** 346 (2011); type: Trinidad & Tobago, Tobago, Parish of St. Paul, along Roxborough–Parlatuvier Road, 11°16·80′N, 60°36·66′W, 500–520 m alt., on tree trunk in rainforest, 12-03-2008, *S. Rui & E. Timdal* 10764 (O L152061!—holotype; CANB!—isotype) (TLC: perlatolic acid, hyperlatolic acid, superlatolic acid).

We have unpublished sequences of the holotype which show that this species does not belong in *Phyllopsora*.

Phyllopsora wellingtonii (Stirt.) Müll. Arg.

Bull. Herb. Boissier **2**(App. 1)**:** 45 (1894).—*Psoromidium wellingtonii* Stirt., *Proc. Roy. Philos. Soc. Glasgow* **10:** 304 (1877); type: not seen (see Galloway & James 1985).

This species belongs in *Psoromidium* and is a synonym of *Psoromidium aleuroides* (Stirt.) D.J. Galloway (Galloway & James 1985; Brako 1989).

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Authors' Contributions

ET and MB planned the study. ET, JH, MC and SK planned and conducted the fieldwork. MC and JH provided collection and export permits for Brazil and Venezuela, respectively. MB and SK generated DNA sequences. SK conducted the phylogenetic analyses under the guidance of SE. SK wrote the first draft and ET wrote the Taxonomy section. All authors corrected and completed the manuscript.

Supplementary Material

For supplementary material accompanying this paper visit https://doi.org/10.1017/S0024282919000252

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