SYSTEMATICS AND PHYLOGENY

Species delimitation at a global scale reveals high species richness with complex biogeography and patterns of symbiont association in *Peltigera* section *Peltigera* (lichenized Ascomycota: Lecanoromycetes)

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Abstract This comprehensive phylogenetic revision of sections *Peltigera* and *Retifoveatae* of the cyanolichen genus *Peltigera* is based on DNA sequences from more than 500 specimens from five continents. We amplified five loci (nrITS, β-tubulin and three intergenic spacers part of colinear orthologous regions [COR]) for the mycobiont, and the *rbcLX* locus for the cyanobacterial partner *Nostoc*. Phylogenetic inferences (RAxML, BEAST) and species delimitation methods (bGMYC, bPTP, bPP) suggest the presence of 88 species in section *Peltigera*, including 50 species new to science, hence uncovering a surprisingly high proportion of previously unnoticed biodiversity. The hypervariable region in ITS1 (ITS1-HR) is a powerful marker to identify species within sections *Peltigera* and *Retifoveatae*. Most newly delimited species are restricted to a single biogeographic region, however, up to ten species have a nearly cosmopolitan distribution. The specificity of mycobionts in their association with *Nostoc* cyanobionts ranges from strict specialists (associate with only one *Nostoc* phylogroup) to broad generalists (up to eight *Nostoc* phylogroups uncovered), with widespread species recruiting a broader selection of *Nostoc* phylogroups than species with limited distributions. In contrast, species from the *P. didactyla* clade characterized by small thalli and asexual vegetative propagules (soredia) associate with fewer *Nostoc* phylogroups (i.e., are more specialized) despite their broad distributions, and show significantly higher rates of nucleotide substitutions.

Keywords collinear orthologous region; COR; cyanobiont; internal transcribed spacer; ITS1-HR; ITS1 hypervariable region; lichen; mycobiont; *Nostoc*; molecular systematics; Peltigerales; phylogeny; rates of evolution; specificity; symbiosis

Supplementary Material The Electronic Supplement (Tables S1–S6; Figs. S1, S2) and DNA sequence alignments are available from https://doi.org/10.12705/675.3.S1 and https://doi.org/10.12705/675.3.S2, respectively.

INTRODUCTION

Peltigera Willd. (Lecanoromycetes: Peltigerales) is a genus of lichen-forming fungi (mycobionts) found in associations with cyanobacteria (cyanobionts) from the genus *Nostoc* Vaucher ex Bornet & Flahault. While most *Peltigera* species associate with *Nostoc* only (bi-membered thalli), a few species associate with a green alga of the genus *Coccomyxa* Schmidle as their main photobiont, and *Nostoc* as their secondary photobiont (tri-membered thalli) (Vitikainen, 1994; Miadlikowska & Lutzoni, 2000). *Peltigera* sect. *Peltigera* (the *canina* group) is one of eight sections of the genus *Peltigera* (Miadlikowska & Lutzoni, 2000). It is characterized mostly by the presence of a tomentum on the upper surface of thalli and by the lack of secondary metabolites detectable by thin-layer chromatography (Holtan-Hartwig, 1993; Vitikainen, 1994; Miadlikowska & al., 2003). The sister section *Retifoveatae* Miądl. & Lutzoni was circumscribed to accommodate a single species (*P. retifoveata* Vitik.) with a distinct and rich chemical profile (Holtan-Hartwig, 1993; Miadlikowska & Lutzoni, 2000). Both sections contain exclusively bi-membered cyanolichens (Miadlikowska & Lutzoni, 2000; Miadlikowska & al., 2003).

Section *Peltigera* includes the emblematic *P. canina* (L.) Willd., type of the genus and one of the first three *Peltigera* species formally described by Linnaeus (1753) as *Lichen caninus*. It comprises thirty of the sixty-six species considered by Martínez & al. (2003) in their worldwide biogeographical study of the genus. Members of section *Peltigera* are found world-wide, with fifteen species in South America and Asia, thirteen in North America, ten in Europe, and nine in Africa and in Australia-New

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Zealand (Vitikainen, 1994, 1998; Brodo & al., 2001; Martínez & al., 2003). Within the last 25 years, ten new species have been described in this section, including five from Papua New Guinea: *P. fimbriata* Vitik. & al., *P. granulosa* Sérus. & al., *P. koponenii* Sérus. & al., *P. montis-wilhelmii* Sérus. & al., and *P. papuana* Sérus. & al. (Sérusiaux & al., 2009); two from China: *P. wulingensis* L.F.Han & S.Y.Guo (Han & al., 2013) and *P. isidiophora* L.F.Han & S.Y.Guo (Han & al., 2015); one from Africa: *P. lambinonii* Goffinet (= *P. sorediifera* (Nyl.) Vitik.; Goffinet & Hastings, 1995); and two from North America and Iceland: *P. castanea* Goward & al. (Goffinet & al., 2003) and *P. islandica* T.Goward & S.S.Manoharan-Basil (Manoharan-Basil & al., 2016). Overall, three species (*P. canina*, *P. didactyla* (With.) J.R.Laundon, *P. rufescens* (Weiss) Humb.) have been reported on all six continents (excluding Antarctica) and five additional species (*P. degenii* Gyeln., *P. lepidophora* (Vain.) Bitter, *P. membranacea* (Ach.) Nyl., *P. praetextata* (Flörke ex Sommerf.) Zopf, *P. ulcerata* Müll.Arg.) were reported from at least four continents (Martìnez & al., 2003). Most of these morphologically delineated species were validated phylogenetically but based only on a few collections and using ribosomal loci exclusively (Miadlikowska & Lutzoni, 2000; Goffinet & al., 2003; Miadlikowska & al., 2003; Sérusiaux & al., 2009; Han & al., 2013; Manoharan-Basil & al., 2016; Jüriado & al., 2017; but see O'Brien & al., 2009).

Because many species of section *Peltigera* have large foliose thalli and are common, especially in the boreal biome, they were often the focus of a wide range of studies, e.g., symbionts culture-based experiments (Miao & al., 1997), patterns of host specialization (O'Brien & al., 2005, 2013), genome sequencing (Xavier & al., 2012), characterization of lectins (Lehr & al., 1995; Díaz & al., 2011; Manoharan & al., 2012), nitrogen fixation estimates and chlorophyll contents (Henriksson & Pearson, 1981; Darnajoux & al., 2017), bioaccumulation of metals (Haas & al., 1998; Darnajoux & al., 2015), and phytase activity (Higgins & Crittenden, 2015). Earlier phylogenetic studies on the genus *Peltigera* focused mostly on species complexes (Goffinet & al., 2003; O'Brien & al., 2009), and rarely covered entire sections (Miadlikowska & al., 2003). In each of the most recent multilocus phylogenetic revisions of specific sections of the genus *Peltigera* (i.e., *P.* sect. *Polydactylon* Miądl. & Lutzoni, sect. *Peltidea* (Ach.) Vain., sect. *Chloropeltigera* Gyeln.), at least one cosmopolitan morphospecies was shown to represent several distinct, and morphologically cryptic, evolutionary lineages (Magain & al., 2017a, b; Pardo-De la Hoz & al., in press; Miadlikowska & al., unpub.).

Section *Peltigera* includes species with different types of reproductive structures. For example, *P. canina* and *P. membranacea* produce numerous apothecia (ascomata) and, therefore, are assumed to reproduce mostly sexually. Other species develop various types of vegetative propagules that contain the fungal and cyanobacterial partners, such as phyllidia (e.g., *P. praetextata*), isidia (e.g., *P. evansiana* Gyeln., *P. lepidophora*), and soredia (e.g., *P. didactyla*, *P. extenuata* (Nyl. ex Vain.) Lojka, *P. ulcerata*) (Vitikainen, 1994; Goward & al., 1995; Goffinet & al., 2003). Despite the presence of asexual propagules, apothecia can also be frequent in some species (e.g., *P. didactyla* or *P. praetextata*). It is assumed that all species can potentially disperse through simple thallus fragmentation. The mode of reproduction in lichens can affect genetic diversity of both main partners and the specificity of their interactions (Otálora & al., 2010, 2013b; Dal Grande & al., 2012; Pardo-De la Hoz & al., in press). Asexual reproduction seems to lead to lower genetic diversity of the two partners, as symbiotic propagules foster vertical transmission of the photobiont. Sexual reproduction of the fungal partner involves an aposymbiotic phase (i.e., horizontal transmission of the photobiont), when the fungus must re-establish a symbiosis with a photosynthetic partner after each ascospore dispersion event. Furthermore, the identity of the symbiotic partners and their patterns of association are likely to drive macroevolutionary trends such as their diversification and evolutionary rates (Magain & Sérusiaux, 2014; Schneider & al., 2016; Magain & al., 2017a).

In *Peltigera-Nostoc* associations, *Peltigera* species are often more specialized than their cyanobiont partners (O'Brien & al., 2013; Magain & al., 2017a; Chagnon & al., 2018; Lu & al., 2018). However, mycobiont specificity is highly variable in section *Polydactylon*, ranging from highly specialized species, i.e., always associating with the same phylogroup of *Nostoc* (monophyletic group of *Nostoc* based on *rbcLX* phylogeny), to generalist species, i.e., associating with several distinct *Nostoc* phylogroups (Magain & al., 2017a). Generalist species generally show broader distribution ranges than specialists, seem to be more recently established, and genetically diverse. Chagnon & al. (2018) found that interactions between species of *P.* sect. *Polydactylon* and *Nostoc* phylogroups were highly modular and anti-nested, indicating strong preferences in interactions. Furthermore, when considering *Peltigera* communities at a local scale, they found associations to be asymmetric, with generalist *Nostoc* partners interacting with specialized *Peltigera* species, but this asymmetry was not detected at a global spatial scale. At an intrabiome scale (boreal biome in Québec, Canada), Lu & al. (2018) reported that *Peltigera* species had narrower ranges and showed a high degree of specialization towards more widespread generalist *Nostoc* phylogroups, and that bioclimatic factors were more limiting in the mycobiont distributions than the availability of cyanobionts. A recent study in Estonia (Jüriado & al., 2017) found most species of section *Peltigera*, many of which were undescribed, to have narrow habitat requirements. Pardo-De la Hoz & al. (in press) showed that the widespread, more temperate, species of section *Chloropeltigera* associate with more *Nostoc* phylogroups and show higher level of genetic diversity than the more boreal species of the sister section *Peltidea*. Based on these previous studies, we expect species from section *Peltigera* to be mainly generalists because many are widespread temperate species.

A nuclear ribosomal ITS- and LSU-based phylogenetic study of section *Peltigera* revealed several undescribed lineages that might represent new species (Miadlikowska & al., 2003). The recent discovery of multiple new species in every section of the genus revised up to date (Miadlikowska & al., 2014a, unpub.; Magain & al., 2017a, b; Pardo-De la Hoz & al., in press), supports the expectation of high species richness in section *Peltigera*. The goals of this study were to: (1) provide

a worldwide comprehensive phylogeny for species of section *Peltigera* based on five molecular markers, including three recently developed and tested collinear orthologous regions (COR) that each include an intergenic spacer; (2) re-evaluate the currently recognized species using species discovery and species validation approaches to assess the level of hidden biodiversity in this section; (3) reveal the patterns of specificity between *Peltigera* species from this section and their *Nostoc* phylogroups (based on the *rbcLX* locus), and compare with the patterns of association detected in other sections of the genus *Peltigera*; and (4) to determine if the reproductive mode (primarily sexual versus asexual) of the mycobiont impacts specificity pattern as well as rates of nucleotide substitution and species diversification in section *Peltigera*.

■ MATERIALS AND METHODS

Taxon sampling and data acquisition. — More than 500 specimens of *Peltigera* sect. *Peltigera* and sect. *Retifoveatae* (identified as such based on morphology) were selected from several herbaria world-wide (AMNH, B, CDS, CGMS, CONC, CONN, DUKE, H, KW, LG, MAF, MEXU, NY, QFA, UBC, UDBC, UGDA, UMEX, UPS, WIS) or were collected during numerous field trips part of this study (Norway, Canada [Québec], and U.S.A. [North Carolina, Alaska] in 2011; Russia, Colombia, Peru, and Brazil in 2012; U.S.A. [Utah], Canada [Alberta], and Ecuador in 2013; Canada [British Columbia] in 1998–2016). We extracted DNA from 375 specimens (Appendix 1; Electr. Suppl.: Table S1) using a modified protocol from Zolan & Pukkila (1986) with a 2% sodium dodecyl sulphate (SDS) as the extraction buffer. For the mycobiont, we targeted five molecular markers. We amplified ca. 0.6 kb of the internal transcribed spacer (ITS) of the nuclear ribosomal tandem repeat using the ITS1F (Gardes & Bruns, 1993) and ITS4 (White & al., 1990) primers; ca. 0.7 kb of β-tubulin using the reverse primer BT2B (Glass & Donaldson, 1995) and the forward primer T1 (O'Donnell & Cigelnik, 1997) or alternatively bt_34F (O'Brien & al., 2009); and three collinear orthologous regions (COR) each including an intergenic spacer (Magain & al., 2017b): COR1b using primers COR-1bF and COR-1bR-B; COR3 using primers COR-3F-A and COR-3R-B; and COR16 using primers COR-16Fout and COR-16Rmid1. For the cyanobiont, we sequenced ca. 1.0 kb of the *rbcLX* region (which includes the last 82 amino acids of the RUBISCO large subunit [*rbcL*], a putative chaperone gene [*rbcX*] and two intergenic spacers; Li & Tabita, 1997) using primers CW and CX, following Rudi & al. (1998). PCR conditions for ITS and *rbcLX* follow Magain & al., 2017a and literature cited therein. β-tubulin and the three COR markers were amplified using the following conditions: 94°C for 30 s, 55°C for 30 s (−0.4°/cycle), 72°C for 1 min (+2 s/cycle) for 24 cycles; 94°C for 30 s, 45°C for 30 s, 72°C for 2 min (+3 s/cycle) for 12 cycles; 72°C for 10 min, followed by storage at 4°C. All PCR amplicons were cleaned with ExoSAP (Affymetrix, Santa Clara, California, U.S.A.) following the manufacturer's protocol. Sequencing was carried out in 10 µl reactions using the same primers as for PCR amplification in the following proportions: 1 µl primer (10 µmol/l), 1 µl purified PCR product, 0.75 µl Big Dye (Big Dye Terminator Cycle sequencing kit, ABIPRISM v.3.1; Perkin-Elmer, Applied Biosystems, Foster City, California, U.S.A.), 3.25 µl Big Dye buffer, and 4 µl double-distilled water. Automated reaction cleanup and visualization was performed at the Duke Genome Sequencing and Analysis Core Facility of the Institute for Genome Sciences and Policies (for details see Gaya & al., 2012).

All newly acquired sequences were subjected to BLAST searches to confirm the fungal or cyanobacterial origin of each sequence fragment. They were assembled and edited using the software package Sequencher v.4.1 (GeneCodes, 2000) and aligned manually with the program MacClade v.4.08 (Maddison & Maddison, 2005). The "Nucleotide with AA color" option was used for guiding all alignments for protein-coding genes, including the delimitation of exons and introns. Ambiguously aligned regions sensu Lutzoni & al. (2000) were delimited manually and excluded from subsequent analyses.

Phylogenetic analyses of the mycobiont datasets. — For *Peltigera* we generated a total of 1273 sequences: 318 ITS, 199 β-tubulin, 252 COR1b, 251 COR3 and 253 COR16 (Appendix 1; Electr. Suppl.: Table S1). We also used sequences of ITS and β-tubulin from other studies (O'Brien & al., 2009; Sérusiaux & al., 2009; Han & al., 2015; Manoharan-Basil & al., 2016) available in GenBank for a total of 357 ITS and 245 β-tubulin sequences used for this study. Prior to data concatenation, single-locus phylogenies were generated for all five fungal loci using RAxML-HPC2 v.7.2.8 (Stamatakis, 2006; Stamatakis & al., 2008) as implemented on the CIPRES portal (Miller & al., 2010). Searches for optimal tree and bootstrap analyses were conducted with the rapid hill-climbing algorithm for 1000 replicates with the GTRGAMMA substitution model (Rodriguez & al., 1990). To detect topological incongruence among single-locus datasets, a reciprocal 70% maximum likelihood (ML) bootstrap support criterion was implemented (Mason-Gamer & Kellogg, 1996; Reeb & al., 2004). The single-locus topologies (Electr. Suppl.: Fig. S1A–E) were considered congruent and we proceeded to concatenation.

The concatenated dataset included specimens with at least two of the five targeted loci, except for a few specimens of *P. fimbriata* and *P. isidiophora* for which only ITS was available. Five outgroup species representing section *Peltidea* (*P. aphthosa* (L.) Willd., *P. malacea* (Ach.) Funck) and section *Polydactylon* (*P. hymenina* (Ach.) Delise, *P. polydactylon* (Neck.) Hoffm., *P. scabrosa* Th.Fr.) were selected for a total of 303 specimens (Appendix 1; Electr. Suppl.: Table S1). Out of 298 ingroup specimens, the following sequences were missing: 4 ITS (1.3%), 59 β-tubulin (19.8%), 51 COR1b (17.1%), 49 COR3 (16.4%) and 46 COR16 (15.4%) sequences. A total of 176 specimens (59.1%) were represented by all five loci, 71 (23.8%) by four loci, 21 (7%) by three loci, 24 (8%) by two loci, and 6 (2%) by a single locus. Section *Retifoveatae* had the largest amount of missing data (26.7%), whereas in section *Peltigera* the proportion of missing data was clade-dependent and varied from 4.8% to 20.8%. We used PartitionFinder v.1.0.1. (Lanfear & al., 2012) on a concatenated dataset with no missing data, to determine the best partitioning scheme and the optimal models

to be used in subsequent multi-locus phylogenetic analyses. The following ten data subsets were pre-delimited: ITS1, ITS2, 5.8S, β-tubulin 1st, 2nd and 3rd codon positions, and non-coding regions (introns), COR1b, COR3, COR16. We then reinserted all specimens for which we had sequences of at least two loci, using the *compare_and_choose* function of the PLexus PERL package (Magain, 2018), into a five-locus dataset. The best partitioning scheme for this global dataset included three subsets: ITS1 and ITS2 (with TVMef+I+Γ as the best model); 5.8S and the 1st and 2nd codon positions of β-tubulin (with JC as the best model); and a third subset with the 3rd codon position, as well as the non-coding regions of β-tubulin, COR1b, COR3 and COR16 (with HKY+Γ as the best model). We performed maximum likelihood searches for the optimal tree and bootstrap analyses (1000 replicates; GTRGAMMA substitution model) using RAxML v.7.4.2 (Stamatakis 2006; Stamatakis & al., 2008). We also ran Bayesian analyses for 40 million generations, sampling every 1000th generation with MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001) as implemented on the CIPRES portal. Two independent runs, each composed of four chains, were completed. We assessed the convergence of chains using Tracer v.1.5 (Rambaut & Drummond, 2007) and Are We There Yet (AWTY; Nylander & al., 2008) as implemented on the website http://king2.scs.fsu.edu/CEBProjects/awty/awty_start.php (last accessed 8 Feb 2017 [website no longer available]).

Using the resulting concatenated five-locus phylogeny, we divided the dataset into nine subsets corresponding to well-supported major clades (1–9, Fig. 1). Species delimitations were performed on subclades of the section and separate RAxML analyses were performed on clades 4 to 9 (clades 1–3 contain only a few specimens representing the early evolutionary splits in the section; see Results section) using the same settings as for the complete dataset. An additional analysis was performed on a dataset comprising clades 4–7, with the same settings, to test for differences in evolutionary rates among these clades.

Species delimitation methods. — For clades 4–9, each of the five loci was analyzed separately (except β-tubulin for clade 4, because of the large amount of missing data), for a total of 29 analyses. BEAST v.1.7 (Drummond & Rambaut, 2007) was used to analyze the following partitioned datasets: for ITS: ITS1, ITS2, 5.8S; for β-tubulin: each codon and non-coding regions; no partitions for COR1b, COR3, COR16. Optimal evolutionary models were selected with MrModeltest v.2 (Nylander, 2004). Bayesian analyses were run for 20 million generations sampling every 200,000th generation. These analyses generated sets of 100 trees each. For each of these tree sets, we completed a bGMYC analysis (Pons & al., 2006; Reid & Carstens, 2012) for 50,000 generations with a burn-in of 40,000 generations, a thinning value of 100 and thresholds values of 2 and 20. We considered a species to be well delimited by bGMYC v.1.0 when the probability of grouping a set of haplotypes together was higher than the probability of any alternative grouping that included at least one haplotype from this putative species (Electr. Suppl.: Table S2). We also used bPTP v.0.51 (Zhang & al., 2013) on the best ML tree resulting from the concatenated analysis as implemented on http://species.h-its.org/ (last accessed on 7 Feb 2017) using default parameters.

We used bPP v.2.2 (Yang & Rannala, 2010) to validate species delimitations obtained with bGMYC and bPTP. Specimens were grouped in a distinct lineage for the bPP analyses if at least two of the species discovery methods (any of the five bGMYC analyses on each locus separately and/or the bPTP analysis on the concatenated dataset) suggested they should be considered as distinct species. For each subset, we ran bPP for 100,000 generations, sampling every 2nd generation, with a burn-in of 2000. Relative nucleotide substitution rates of the loci were estimated using the best topologies resulting from single-loci ML analyses. We repeated the analyses for a wide variety of θ and τ values and examined the changes in the likelihood, as well as the difference between the prior values of θ (as defined by the prior distribution) and the posterior values of θ as averaged from the θ values estimated for each branch (Electr. Suppl.: Table S3).

Testing for differential nucleotide substitution rates. — We implemented PAML v.4.8a (Yang, 1997) on the best ML tree reconstructed from a subset of clades 4–7 where we kept one representative per species (as delimited in this study; see Results section) to compare evolutionary rates between the clade comprising sorediate species (clade 4) and the remaining clades in the tree. We ran likelihood ratio tests (LRT) to compare the different scenarios using the best tree with either a strict molecular clock, several scenarios of local clocks along the tree, or no clock (Table 1).

Biogeographical analyses. — For each species delimited as part of this study, we selected specimens for which at least four loci were available. If this was not possible, we selected specimens with the highest number of loci. For computational purposes, and to prevent the dataset to be too asymmetrical, we further pruned the dataset. For species represented by more than five specimens, we kept the specimens according to the following selection scheme: highest number of loci, unique geographic origin, and unique phylogenetic placement. Our final adjusted five-locus matrix consisted of 225 specimens representing 90 species. We ran a Bayesian analysis using BEAST v.2.4.5 (Bouckaert & al., 2014) for 50 million generations, sampling every 1000th generation, using unlinked substitution models, a lognormal relaxed clock linked among loci, and linked trees. MrModeltest2 (Nylander, 2004) estimated the best substitution models to be: GTR+I+Γ for ITS, HKY+I+Γ for β-tubulin, and HKY+Γ for COR1b, COR3 and COR16. We collapsed branches within each species (single branch per species) using Mesquite v.3.11 (Maddison & Maddison, 2015).

We performed biogeographic history analyses on the resulting tree using the R package BioGeoBEARS v.0.2.1 (Matzke, 2013a, b). We delimited nine geographic regions and allowed a maximum of six geographic regions per species or node because of computational limitations. Regions were delimited as follows: Europe, North America, Asia (excluding Indonesia and the Philippines), Africa, Australasia (including Australia, New Zealand, Papua New Guinea, Indonesia and the Philippines), Neotropics (from Mexico to Brazil), Neantarctic (Argentina, Chile), Panboreal (boreal regions of Europe, North America and Asia) and Pacific Northwest (Oregon, Washington, British Columbia). Defined regions follow the observations of distribution patterns of *Peltigera* species in other sections (e.g., Magain

Table 1. Likelihood scores for the best ML tree resulting from an analysis on clades 4–7 under different rate conditions.

Rates	Scenario no.	Clade 4	Clade 5	Clade 6	Clade 7	No. of rates	lnL
Molecular clock	1	r1	r1	r1	r1	1	−16855.64734
Local clock in clade 4	2	r1	r2	r2	r2	2	**−16737.61097**
Local clock in clade 5+6	3	r1	r2	r2	r1	2	−16760.69642
Local clock in clade 7	4	r1	r1	r1	r2	2	−16766.77956
Local clock in clade 6	5	r1	r1	r2	r1	2	−16768.69647
Local clock in clade 5	6	r1	r2	r1	r1	2	−16774.92650
Local clocks in clade 4 and in clade 5+6	7	r1	r2	r2	r3	3	−16737.60911
No clock	8	NA	NA	NA	NA	equal to no. of branches	**−16605.81107**

Bold values indicate the best likelihood score overall and the best likelihood score with two rate parameters. NA, not applicable.

& al., 2017a). We tested six models: DEC, DEC+J (Ree & Smith, 2008; Matzke, 2014), and likelihood interpretations of the DIVA (Ronquist, 1997; Ronquist & Sanmartín, 2011) and BAYAREA models (Landis & al., 2013), with and without the J parameter (hereafter referred as DIVALIKE, DIVALIKE+J, BAYAREALIKE and BAYAREALIKE+J). The J parameter represents the relative per-event weight of founder-events (Van Dam & Matzke, 2016).

Phylogenetic analyses of the cyanobiont dataset. — We amplified and sequenced the *rbcLX* locus for 305 cyanobionts directly from the same DNA isolated from lichen thalli, which was used to sequence mycobiont loci (Appendix 1; Electr. Suppl.: Table S1). We added 455 sequences from GenBank resulting in a 759-sequence dataset. Identical sequences were collapsed using the script collapse_multi.pl from the PERL package PLexus v.0.1 (Electr. Suppl.: Table S4), resulting in a final dataset of 437 unique sequences. Ambiguous regions of the alignment (i.e., the two spacers) were excluded from the phylogenetic analyses.

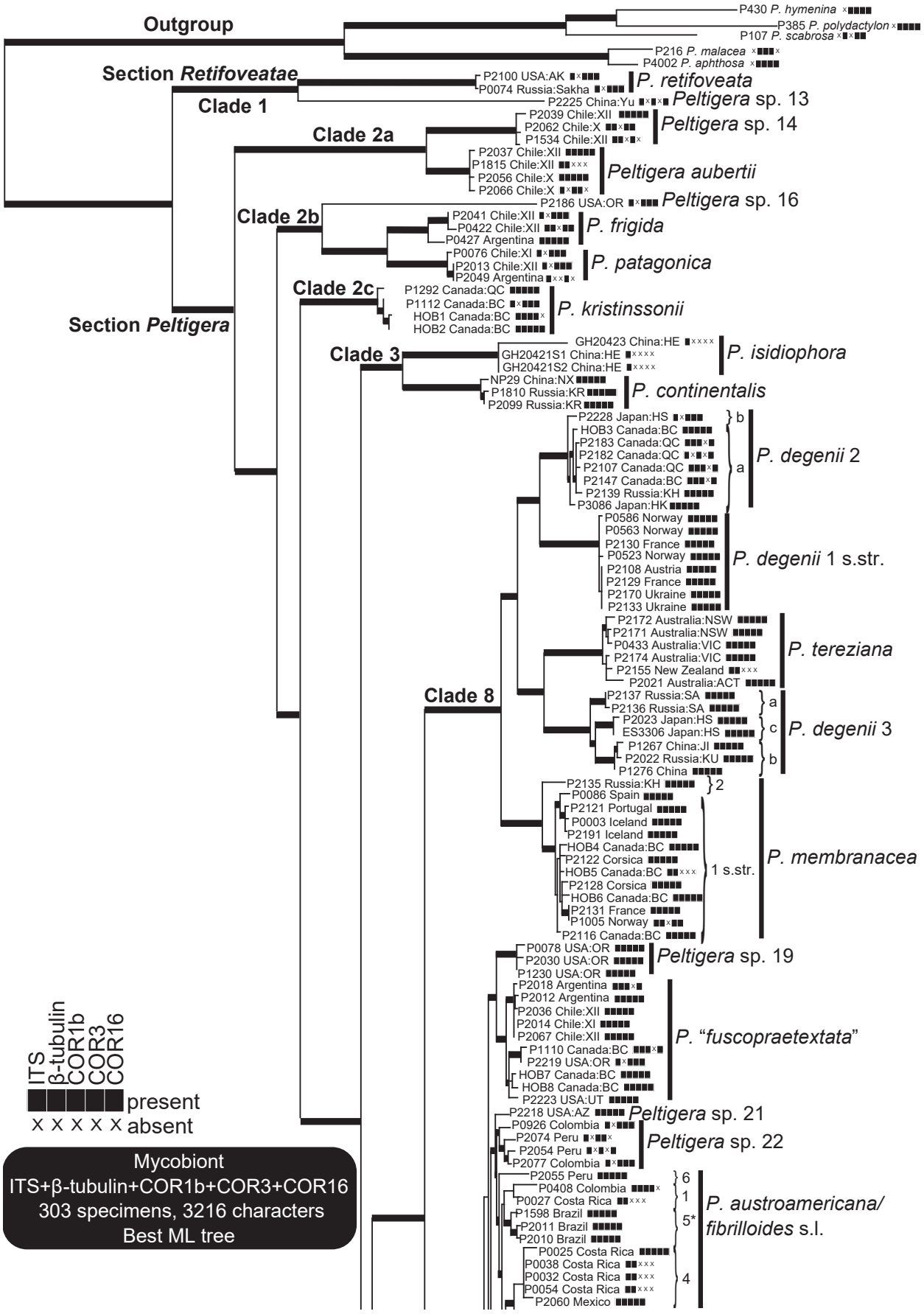
We performed phylogenetic analyses on the *rbcLX* dataset using RAxML-HPC2 v.7.2.8. Optimal tree and bootstrap searches were conducted with the rapid hill-climbing algorithm for 1000 replicates with the GTRGAMMA nucleotide substitution model. The dataset was partitioned according to codon positions, and the best substitution models were determined with MrModeltest2. We ran MrBayes v.3.1.2 as implemented on the CIPRES portal for 50 million generations, sampling every 1000th generation. Two independent runs, each composed of four chains, were performed. We assessed the convergence of chains using Tracer v.1.5 and AWTY as implemented on the website http://king2.scs.fsu.edu/CEBProjects/awty/awty_start.php (last accessed 8 Feb 2017 [website no longer available]). The first 25% of the samples were removed as burn-in.

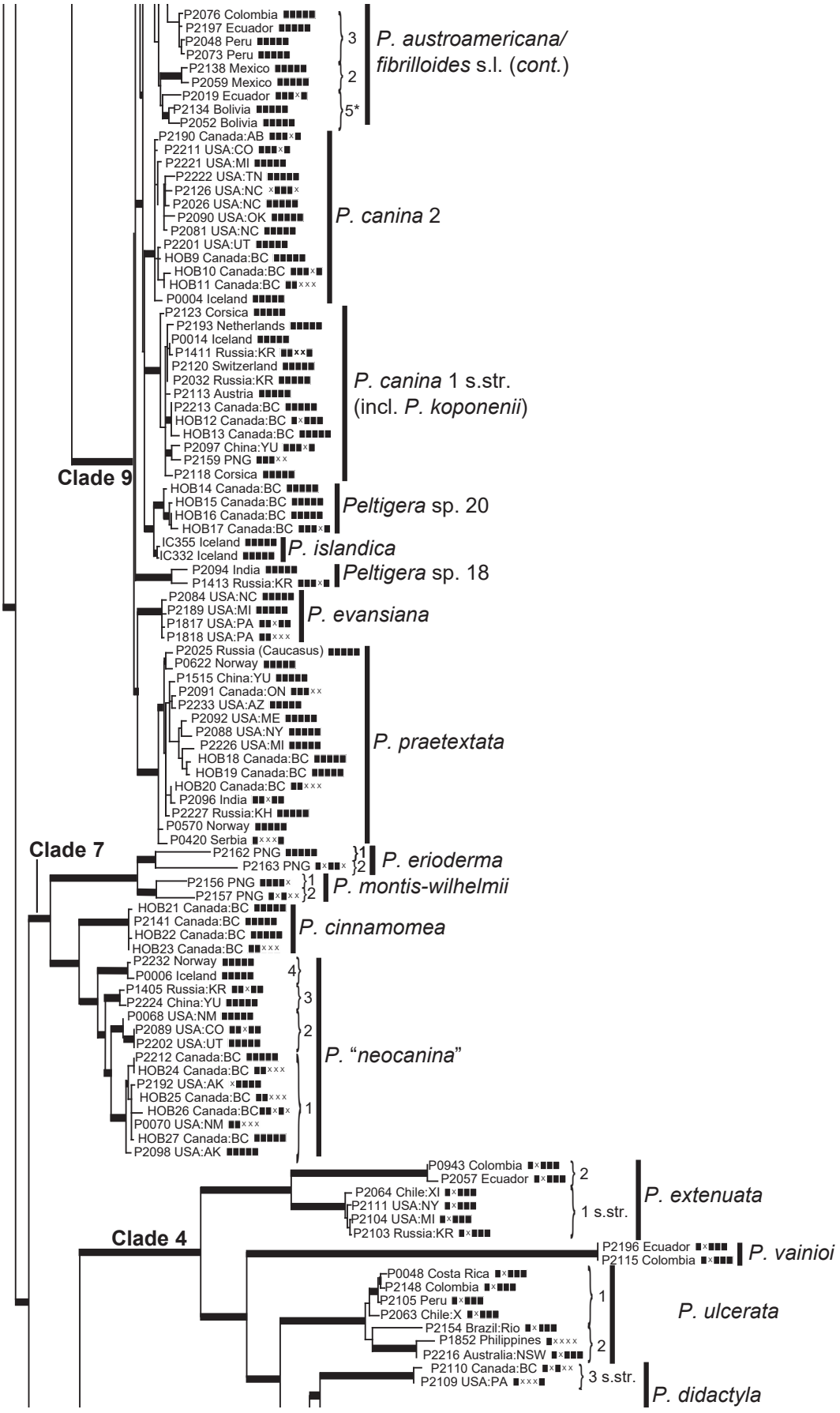
Specificity index. — For each *Peltigera* species for which the cyanobiont's *rbcLX* was sequenced from at least three specimens, we calculated a Specificity index, adapted from Simpson's index (Simpson, 1949), calculated as

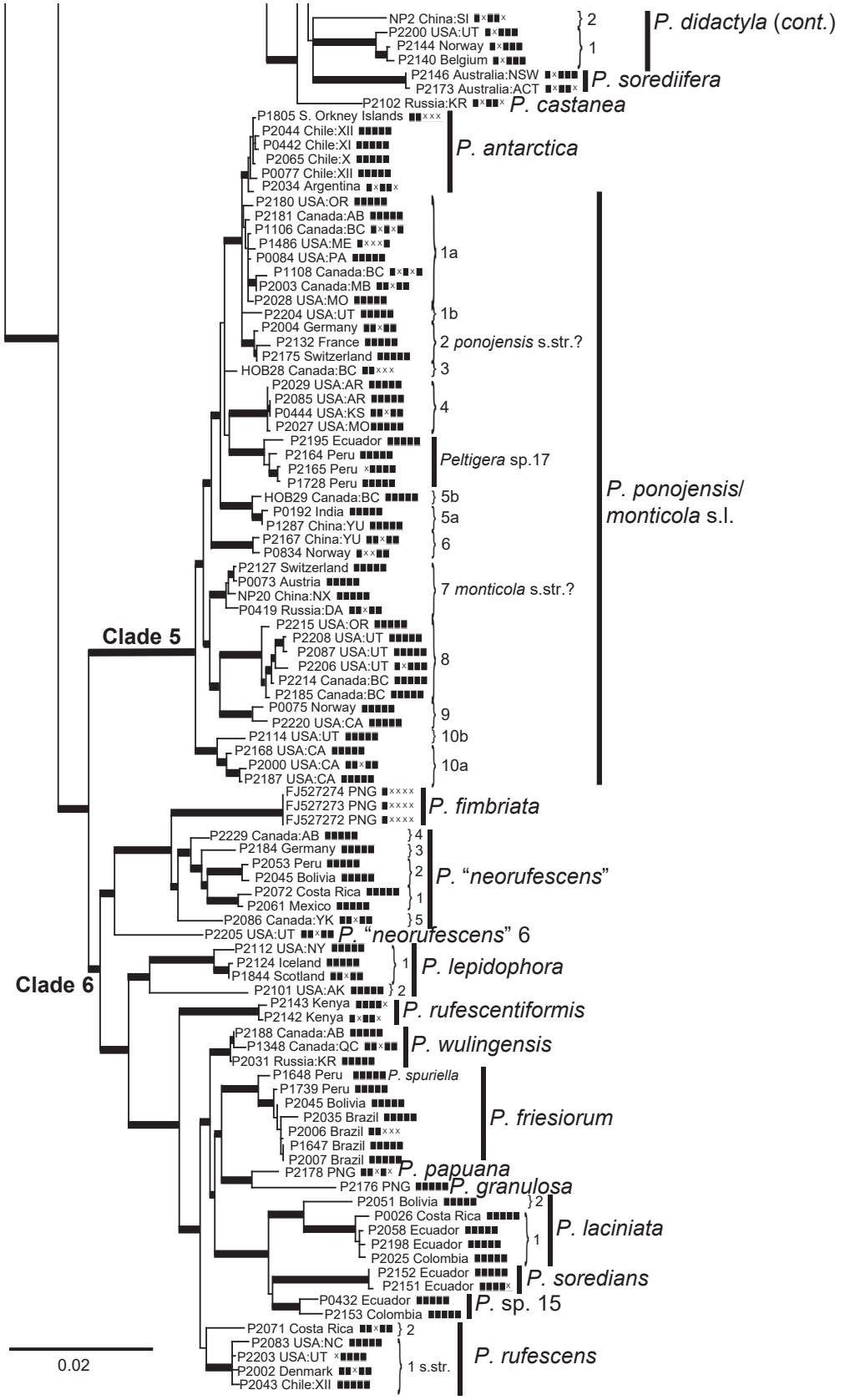
$$\sum_{i=1}^{N} f_i^2$$

where N is the number of *Nostoc* phylogroups that the species associates with, and f_i is the frequency of association with the phylogroup calculated as the number of *rbcLX* sequences from this phylogroup divided by the total number of *rbcLX* sequences available from cyanobionts associated with this *Peltigera* species. With this index, a true *Peltigera* specialist, i.e., a species always associating with the same *Nostoc* phylogroup, has a specificity of 1, whereas a species associating with one phylogroup in half of the thalli and another one in the other half of the specimens would have a value of 0.5. A *Peltigera* species associating with a different phylogroup in each thallus would have a value tending towards 0 with an infinite population size.

Fig. 1. Phylogeny of the genus *Peltigera*, sections *Peltigera* and *Retifoveatae*. Best ML tree resulting from a RaxML analysis on a concatenated dataset of five loci representing 298 specimens and 5 outgroup species from sections *Peltidea* and *Polydactylon* (Appendix 1; Electr. Suppl.: Table S1). The overall rooting of the tree follows Magain & al. (2017a). Black boxes after the reference number and geographic origin of the specimens represent sequenced loci in the following order: ITS, β-tubulin, COR1b, COR3, COR16. Sections were named according to Miadlikowska & Lutzoni (2000) and numbered clades were defined in this study. Thick branches received a bootstrap support ≥70% and Bayesian posterior probability support ≥0.95. The consensus of species delimitations (see Results) is indicated by thick vertical lines and brackets. **P. austroamericana*/*fibrilloides* 5 as delimited by the consensus of methods does not appear monophyletic on this tree. Abbreviations: AB = Alberta, ACT = Australian Capital Territory, AK = Alaska, AR = Arkansas, AZ = Arizona, BC = British Columbia, CA = California, CO = Colorado, DA = Dagestan, HE = Hebei, HK = Hokkaido, HS = Honshu, JI = Jilin, KH = Khabarovsk, KR = Krasnoyarsk, KS = Kansas, KU = Kurile Islands, ME = Maine, MI = Michigan, MO = Missouri, NC = North Carolina, NM = New Mexico, NSW = New South Wales, NY = New York, NX = Ningxia, PA = Pennsylvania, OK = Oklahoma, ON = Ontario, OR = Oregon, PNG = Papua New Guinea, QC = Québec, SA = Sakhalin, SI = Sichuan, TN = Tennessee, UT = Utah, YK = Yukon, YU = Yunnan; X, XI, XII refer to numbers of Chilean Regions as shown in Appendix 1/Electr. Suppl.: Table S1.


Outgroup
P430 P. hymenina
P385 P. polydactylon
P107 P. scabrosa
P216 P. malacea
P4002 P. aphthosa
Section Retifoveatae
P2100 USA:AK
P0074 Russia:Sakha
P. retifoveata
P2225 China:Yu
Peltigera sp. 13
Clade 1
Clade 2a
P2039 Chile:XII
P2062 Chile:X
P1534 Chile:XII
Peltigera sp. 14
P2037 Chile:XII
P1815 Chile:XII
P2056 Chile:X
P2066 Chile:X
Peltigera aubertii
P2186 USA:OR
Peltigera sp. 16
Clade 2b
P2041 Chile:XII
P0422 Chile:XII
P0427 Argentina
P. frigida
P0076 Chile:XI
P2013 Chile:XII
P2049 Argentina
P. patagonica
Clade 2c
P1292 Canada:QC
P1112 Canada:BC
HOB1 Canada:BC
HOB2 Canada:BC
P. kristinssonii
Section Peltigera
GH20423 China:HE
GH20421S1 China:HE
GH20421S2 China:HE
P. isidiophora
Clade 3
NP29 China:NX
P1810 Russia:KR
P2099 Russia:KR
P. continentalis
P2228 Japan:HS
HOB3 Canada:BC
P2183 Canada:QC
P2182 Canada:QC
P2107 Canada:QC
P2147 Canada:BC
P2139 Russia:KH
P3086 Japan:HK
b
a
P. degenii 2
P0586 Norway
P0563 Norway
P2130 France
P0523 Norway
P2108 Austria
P2129 France
P2170 Ukraine
P2133 Ukraine
P. degenii 1 s.str.
P2172 Australia:NSW
P2171 Australia:NSW
P0433 Australia:VIC
P2174 Australia:VIC
P2155 New Zealand
P2021 Australia:ACT
P. tereziana
Clade 8
P2137 Russia:SA
P2136 Russia:SA
P2023 Japan:HS
ES3306 Japan:HS
P1267 China:JI
P2022 Russia:KU
P1276 China
a
c
b
P. degenii 3
P2135 Russia:KH
P0086 Spain
P2121 Portugal
P0003 Iceland
P2191 Iceland
HOB4 Canada:BC
P2122 Corsica
HOB5 Canada:BC
P2128 Corsica
HOB6 Canada:BC
P2131 France
P1005 Norway
P2116 Canada:BC
2
1 s.str.
P. membranacea
P0078 USA:OR
P2030 USA:OR
P1230 USA:OR
Peltigera sp. 19
P2018 Argentina
P2012 Argentina
P2036 Chile:XII
P2014 Chile:XI
P2067 Chile:XII
P1110 Canada:BC
P2219 USA:OR
HOB7 Canada:BC
HOB8 Canada:BC
P2223 USA:UT
P. "fuscopraetextata"
P2218 USA:AZ
Peltigera sp. 21
P0926 Colombia
P2074 Peru
P2054 Peru
P2077 Colombia
Peltigera sp. 22
P2055 Peru
P0408 Colombia
P0027 Costa Rica
P1598 Brazil
P2011 Brazil
P2010 Brazil
P0025 Costa Rica
P0038 Costa Rica
P0032 Costa Rica
P0054 Costa Rica
P2060 Mexico
6
1
5*
4
P. austroamericana/
fibrilloides s.l.
ITS
β-tubulin
COR1b
COR3
COR16
present
absent
Mycobiont
ITS+β-tubulin+COR1b+COR3+COR16
303 specimens, 3216 characters
Best ML tree


P2076 Colombia
P2197 Ecuador
P2048 Peru
P2073 Peru
P2138 Mexico
P2059 Mexico
P2019 Ecuador
P2134 Bolivia
P2052 Bolivia
3
2
5*
P. austroamericana/ fibrilloides s.l. (cont.)
P2190 Canada:AB
P2211 USA:CO
P2221 USA:MI
P2222 USA:TN
P2126 USA:NC
P2026 USA:NC
P2090 USA:OK
P2081 USA:NC
P2201 USA:UT
HOB9 Canada:BC
HOB10 Canada:BC
HOB11 Canada:BC
P0004 Iceland
P. canina 2
P2123 Corsica
P2193 Netherlands
P0014 Iceland
P1411 Russia:KR
P2120 Switzerland
P2032 Russia:KR
P2113 Austria
P2213 Canada:BC
HOB12 Canada:BC
HOB13 Canada:BC
P2097 China:YU
P2159 PNG
P2118 Corsica
P. canina 1 s.str. (incl. P. koponenii)
Clade 9
HOB14 Canada:BC
HOB15 Canada:BC
HOB16 Canada:BC
HOB17 Canada:BC
Peltigera sp. 20
IC355 Iceland
IC332 Iceland
P. islandica
P2094 India
P1413 Russia:KR
Peltigera sp. 18
P2084 USA:NC
P2189 USA:MI
P1817 USA:PA
P1818 USA:PA
P. evansiana
P2025 Russia (Caucasus)
P0622 Norway
P1515 China:YU
P2091 Canada:ON
P2233 USA:AZ
P2092 USA:ME
P2088 USA:NY
P2226 USA:MI
HOB18 Canada:BC
HOB19 Canada:BC
HOB20 Canada:BC
P2096 India
P2227 Russia:KH
P0570 Norway
P0420 Serbia
P. praetextata
Clade 7
P2162 PNG
P2163 PNG
1
2
P. erioderma
P2156 PNG
P2157 PNG
1
2
P. montis-wilhelmii
HOB21 Canada:BC
P2141 Canada:BC
HOB22 Canada:BC
HOB23 Canada:BC
P. cinnamomea
P2232 Norway
P0006 Iceland
P1405 Russia:KR
P2224 China:YU
P0068 USA:NM
P2089 USA:CO
P2202 USA:UT
P2212 Canada:BC
HOB24 Canada:BC
P2192 USA:AK
HOB25 Canada:BC
HOB26 Canada:BC
P0070 USA:NM
HOB27 Canada:BC
P2098 USA:AK
4
3
2
1
P. "neocanina"
P0943 Colombia
P2057 Ecuador
2
P2064 Chile:XI
P2111 USA:NY
P2104 USA:MI
P2103 Russia:KR
1 s.str.
P. extenuata
Clade 4
P2196 Ecuador
P2115 Colombia
P. vainioi
P0048 Costa Rica
P2148 Colombia
P2105 Peru
P2063 Chile:X
P2154 Brazil:Rio
P1852 Philippines
P2216 Australia:NSW
1
2
P. ulcerata
P2110 Canada:BC
P2109 USA:PA
3 s.str.
P. didactyla


NP2 China:SI
P2200 USA:UT
P2144 Norway
P2140 Belgium
2
1
P. didactyla (cont.)
P2146 Australia:NSW
P2173 Australia:ACT
P. sorediifera
P2102 Russia:KR
P. castanea
P1805 S. Orkney Islands
P2044 Chile:XII
P0442 Chile:XI
P2065 Chile:X
P0077 Chile:XII
P2034 Argentina
P. antarctica
P2180 USA:OR
P2181 Canada:AB
P1106 Canada:BC
P1486 USA:ME
P0084 USA:PA
P1108 Canada:BC
P2003 Canada:MB
P2028 USA:MO
1a
P2204 USA:UT
P2004 Germany
P2132 France
P2175 Switzerland
1b
2 ponojensis s.str.?
HOB28 Canada:BC
3
P2029 USA:AR
P2085 USA:AR
P0444 USA:KS
P2027 USA:MO
4
P2195 Ecuador
P2164 Peru
P2165 Peru
P1728 Peru
Peltigera sp.17
HOB29 Canada:BC
5b
P0192 India
P1287 China:YU
5a
P2167 China:YU
P0834 Norway
6
P2127 Switzerland
P0073 Austria
NP20 China:NX
P0419 Russia:DA
7 monticola s.str.?
P. ponojensis/
monticola s.l.
Clade 5
P2215 USA:OR
P2208 USA:UT
P2087 USA:UT
P2206 USA:UT
P2214 Canada:BC
P2185 Canada:BC
8
P0075 Norway
P2220 USA:CA
9
P2114 USA:UT
P2168 USA:CA
P2000 USA:CA
P2187 USA:CA
10b
10a
FJ527274 PNG
FJ527273 PNG
FJ527272 PNG
P. fimbriata
P2229 Canada:AB
P2184 Germany
P2053 Peru
P2045 Bolivia
P2072 Costa Rica
P2061 Mexico
4
3
2
1
P. "neorufescens"
P2086 Canada:YK
5
P2205 USA:UT
P. "neorufescens" 6
P2112 USA:NY
P2124 Iceland
P1844 Scotland
1
P. lepidophora
P2101 USA:AK
2
Clade 6
P2143 Kenya
P2142 Kenya
P. rufescentiformis
P2188 Canada:AB
P1348 Canada:QC
P2031 Russia:KR
P. wulingensis
P1648 Peru
P. spuriella
P1739 Peru
P2045 Bolivia
P2035 Brazil
P2006 Brazil
P1647 Brazil
P2007 Brazil
P. friesiorum
P2178 PNG
P. papuana
P2176 PNG
P. granulosa
P2051 Bolivia
P0026 Costa Rica
P2058 Ecuador
P2198 Ecuador
P2025 Colombia
2
1
P. laciniata
P2152 Ecuador
P2151 Ecuador
P. sorediansP0432 Ecuador
P2153 Colombia
P. sp. 15
P2071 Costa Rica
P2083 USA:NC
P2203 USA:UT
P2002 Denmark
P2043 Chile:XII
2
1 s.str.
P. rufescens
0.02

■ RESULTS

Phylogenetic relationships and species delimitation in *Peltigera* sect. *Peltigera* and sect. *Retifoveatae*. — The monospecific section *Retifoveatae* seems to include a second species (*Peltigera* sp. 13; the numbering of new species follows Magain & al., 2017a, b, who reported 12 new *Peltigera* species for section *Polydactylon*) represented by a single collection from China (clade 1; Fig. 1). The chemistry of this putative new species is similar to the chemistry of *P. retifoveata*. The presence of unique terpenoids was the justification for recognizing a separate section (*Retifoveatae*) for *P. retifoveata* (Miadlikowska & Lutzoni, 2000).

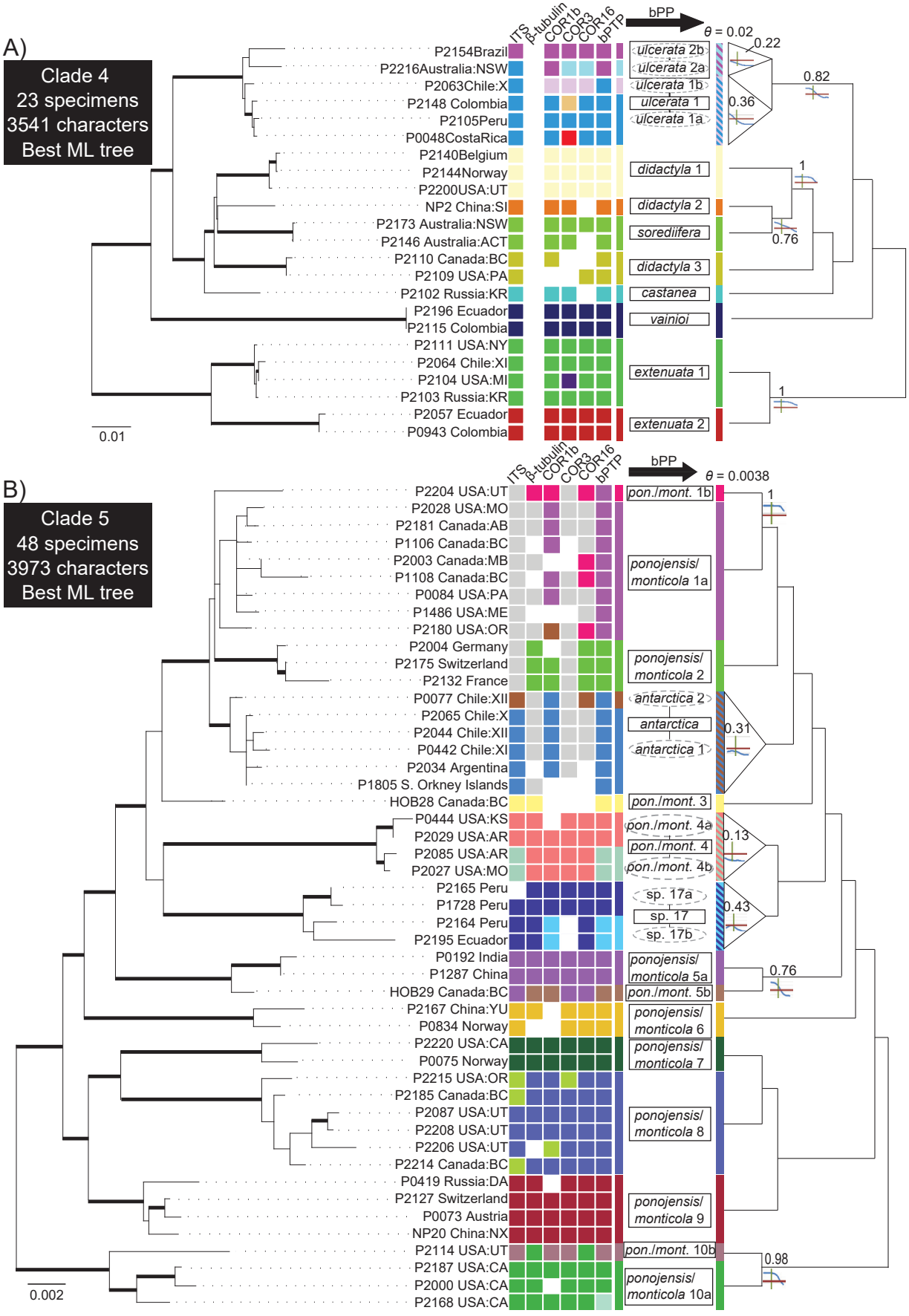
Our results suggest the presence of 50 new species for a total of 88 species in section *Peltigera*. The newly discovered putative species are spread across the section (clades 2 and 3: 2 of 8; clade 4: 4 of 10; clade 5: 11 of 15; clade 6: 10 of 20; clade 7: 6 of 9; clade 8: 6 of 9; clade 9: 11 of 17). Ten major clades are well delimited and highly supported in section *Peltigera* (clades 2a–c, 3–9; Fig. 1); four of them (clades 2a–c, 3) represent lineages from early divergences. The first two divergences (clades 2a and 2b) include (with one exception) specimens from Chile and Argentina representing *Peltigera aubertii* C.W.Dodge and one newly recognized species (*P.* sp. 14 corresponding to *Peltigera* sp. nov. in Miadlikowska & al., 2014a) in clade 2a, and two known species (*P. frigida* R.Sant., *P. patagonica* Räsänen) as well as a putative new species from the Pacific Northwest (Oregon) in clade 2b. The next two divergences include the North American *P. kristinssonii* Vitik. (clade 2c) and an Asian clade of two sister species: *P. continentalis* Vitik. and *P. isidiophora* (clade 3). The remaining six clades (clades 4–9), part of a single monophyletic group, are more species rich and contain multiple unnamed lineages intermixed with known species, some of which are non-monophyletic or are nested within broadly delimited species.

Clade 4. — The *P. didactyla* clade includes 24 specimens (Fig. 1) representing six currently recognized, all sorediate, species (Fig. 1): *P. castanea*, *P. didactyla*, *P. extenuata*, *P. sorediifera*, *P. ulcerata*, and *P. vainioi* Gyeln. Species discovery methods delimited 10 to 14 species in this clade (Fig. 2A; Electr. Suppl.: Table S2). *Peltigera castanea*, *P. sorediifera* and *P. vainioi* were considered well-delimited, whereas each of the remaining three species represents potentially multiple species (*P. didactyla* includes three species, *P. extenuata* includes two, and *P. ulcerata* includes up to four). Twelve lineages were subjected to bPP analyses for validation (Fig. 2A). The final bPP analysis ($\theta = 0.02$; Electr. Suppl.: Table S3) supported the recognition of two putative species within *P. ulcerata* (*P. ulcerata* 1 and 2; Fig. 2A), and validated the remaining eight species.

Clade 5. — The *P. ponojensis* Gyeln./*P. monticola* Vitik. clade includes 48 specimens (Fig. 1) representing three currently recognized species: *P. antarctica* C.W.Dodge, *P. monticola* and *P. ponojensis*. This is one of the two clades (together with clade 9) with the highest level of discrepancy among the results provided by the species discovery methods (11 to 17 species recognized) and with multiple specimens failing to group to a species according to our bGMYC criterion (gray boxes in Fig. 2B; Electr. Suppl.: Table S2). Among the 18 lineages selected to be validated by bPP ($\theta = 0.0038$; Fig. 2B; Electr. Suppl.: Table S3), 15 were confirmed. Two of them represent the new species *P.* sp. 17 and *P. antarctica* as currently circumscribed, whereas specimens identified as *P. monticola* and *P. ponojensis* were assigned to thirteen mostly intermixed putative species (Fig. 2B).

Clade 6. — The *P. rufescens* clade includes 43 specimens (Fig. 1) representing eleven currently recognized species: *Peltigera granulosa*, *P. fimbriata*, *P. laciniata* (G.Merr.) Gyeln., *P. lepidophora*, *P. papuana*, *P. rufescens*, *P. rufescentiformis* (Gyeln.) C.W.Dodge, *P. soredians* Vitik., *P. wulingensis*, specimens that probably correspond to *P. friesiorum* Gyeln. and *P. spuriella* Vain., and a putative species provisionally named *P.* "*neorufescens*" (Miadlikowska & Lutzoni, 2000; Miadlikowska & al., 2003). Species discovery methods suggested the presence of 12 to 19 species. All 19 lineages representing putative species were validated by bPP ($\theta = 0.004$; Fig. 2C) with support values >0.99 (Fig. 2C; Electr. Suppl.: Table S2).

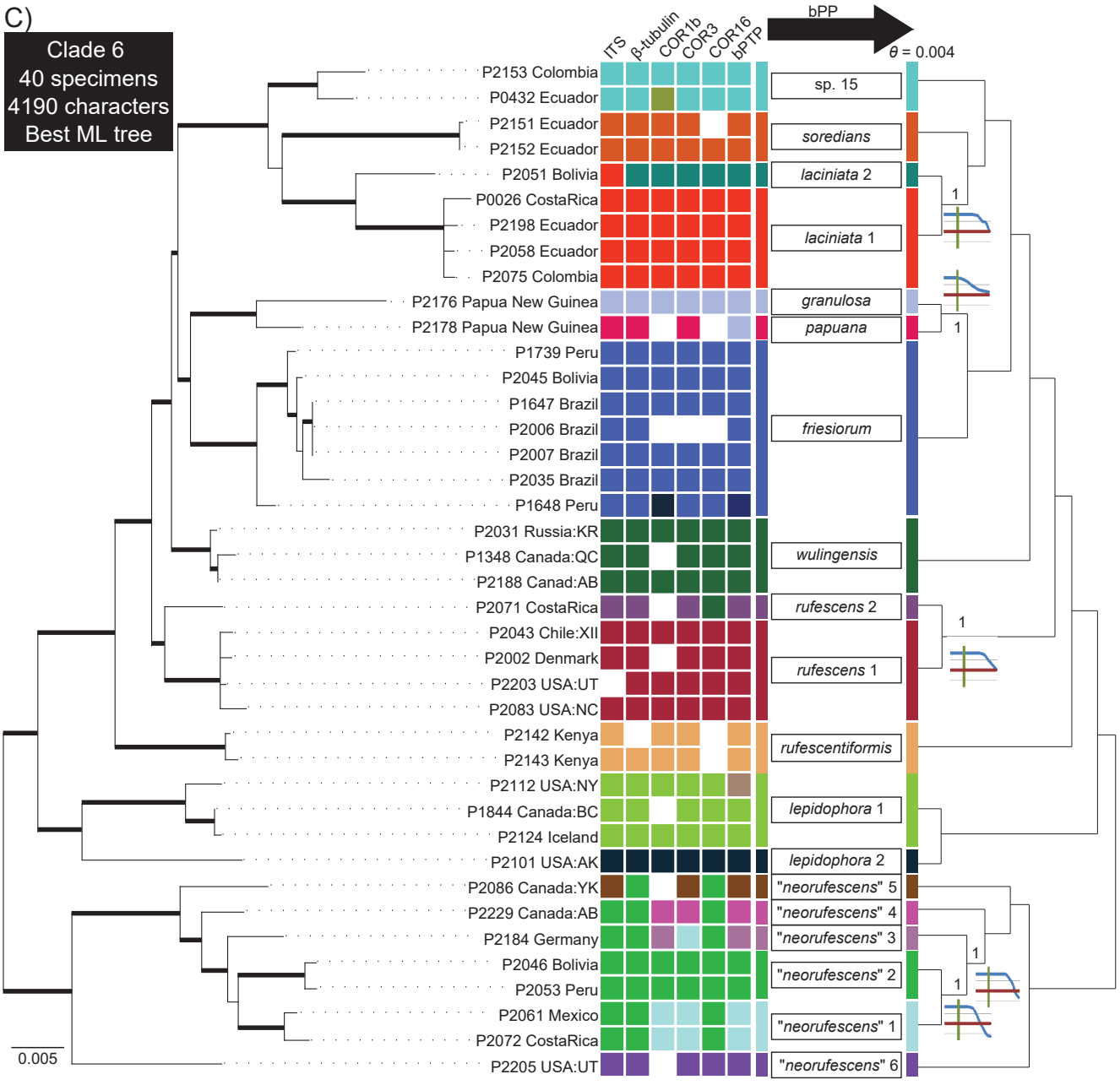
Fig. 2. Comparison of species delimitations resulting from bGMYC analyses on each locus separately and bPTP analyses on members of the following clades within section *Peltigera*: 4 (**A**), 5 (**B**), 6 (**C**), 7 (**D**), 8 (**E**), and 9 (**F**). The left panel on each figure represents the best ML tree where thick branches received bootstrap support ≥70%. Boxes of the same color indicate congruent species delimitation among methods/loci for each specimen. White boxes indicate missing loci. A gradient of two colors represents conflicting species delimitations with similar probability values (see Electr. Suppl.: Table S2). The columns with locus names represent species delimitation with bGMYC. bPTP results were obtained on the best ML tree resulting from the concatenated 5-locus dataset. The color-coded bars to the left of the lineage names, as well as lineage names in dashed ovals, represent species assignments prior to the bPP analysis, whereas the color-coded bars to the right of the lineage names and the lineage names in black boxes represent the final bPP results (mean value of the θ parameter of the final analysis is shown above the color-coded bars). The right panel on each figure represents a schematic species tree where triangles indicate lineages merged by bPP, whereas lines represent species validated by bPP, according to the final bPP analysis. Graphs associated with selected nodes represent the posterior probability of keeping the two species separate (from 0 to 1, Y axis) as a function of the prior mean of the θ value (logarithmic scale, X axis); the horizontal red line represents a PP value of 0.5, whereas the vertical green line represents the θ value chosen for the final analysis (Electr. Suppl.: Table S3). θ values ranges from 0.001 to 0.032 for clades 5, 7, 8 and 9; from 0.01 to 0.1 for clade 4; and from 0.001 to 0.1 for clade 6. Posterior probability values associated with the final analyses are shown above each graph. Abbreviations: AB = Alberta, ACT = Australian Capital Territory, AK = Alaska, AR = Arkansas, AZ = Arizona, BC = British Columbia, CA = California, CC = Caucasus, CO = Colorado, DA = Dagestan, HE = Hebei, HK = Hokkaido, HS = Honshu, JI = Jilin, KH = Khabarovsk, KR = Krasnoyarsk, KS = Kansas, KU = Kurile Islands, ME = Maine, MI = Michigan, MO = Missouri, NC = North Carolina, NM = New Mexico, NSW = New South Wales, NY = New York, NX = Ningxia, PA = Pennsylvania, OK = Oklahoma, ON = Ontario, OR = Oregon, PNG = Papua New Guinea, QC = Québec, SA = Sakhalin, SI = Sichuan, TN = Tennessee, UT = Utah, YK = Yukon, YU = Yunnan; X, XI, XII refer to numbers of Chilean Regions as shown in Electr. Suppl.: Table S1. Specimens in the *ponojensis*/*monticola* clade were abbreviated as *pon.*/*mont.* and *austroamericana*/*fibrilloides* as *austr.*/*fibr.*

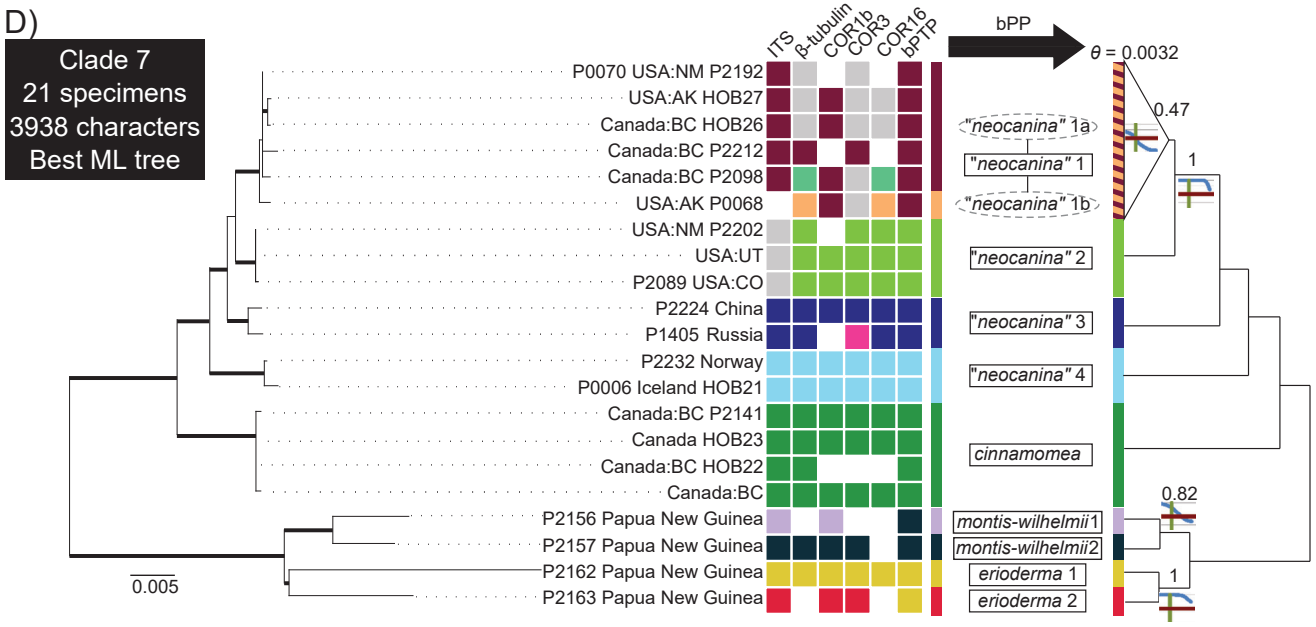

A)
Clade 4
23 specimens
3541 characters
Best ML tree
ITS
β-tubulin
COR1b
COR3
COR16
bPTP
bPP
θ = 0.02
P2154Brazil
P2216Australia:NSW
P2063Chile:X
P2148 Colombia
P2105Peru
P0048CostaRica
P2140Belgium
P2144Norway
P2200USA:UT
NP2 China:SI
P2173 Australia:NSW
P2146 Australia:ACT
P2110 Canada:BC
P2109 USA:PA
P2102 Russia:KR
P2196 Ecuador
P2115 Colombia
P2111 USA:NY
P2064 Chile:XI
P2104 USA:MI
P2103 Russia:KR
P2057 Ecuador
P0943 Colombia
ulcerata 2b
ulcerata 2a
ulcerata 1b
ulcerata 1
ulcerata 1a
didactyla 1
didactyla 2
sorediifera
didactyla 3
castanea
vainioi
extenuata 1
extenuata 2
0.22
0.82
0.36
1
0.76
1
0.01
B)
Clade 5
48 specimens
3973 characters
Best ML tree
bPP
θ = 0.0038
P2204 USA:UT
P2028 USA:MO
P2181 Canada:AB
P1106 Canada:BC
P2003 Canada:MB
P1108 Canada:BC
P0084 USA:PA
P1486 USA:ME
P2180 USA:OR
P2004 Germany
P2175 Switzerland
P2132 France
P0077 Chile:XII
P2065 Chile:X
P2044 Chile:XII
P0442 Chile:XI
P2034 Argentina
P1805 S. Orkney Islands
HOB28 Canada:BC
P0444 USA:KS
P2029 USA:AR
P2085 USA:AR
P2027 USA:MO
P2165 Peru
P1728 Peru
P2164 Peru
P2195 Ecuador
P0192 India
P1287 China
HOB29 Canada:BC
P2167 China:YU
P0834 Norway
P2220 USA:CA
P0075 Norway
P2215 USA:OR
P2185 Canada:BC
P2087 USA:UT
P2208 USA:UT
P2206 USA:UT
P2214 Canada:BC
P0419 Russia:DA
P2127 Switzerland
P0073 Austria
NP20 China:NX
P2114 USA:UT
P2187 USA:CA
P2000 USA:CA
P2168 USA:CA
pon./mont. 1b
ponojensis/ monticola 1a
ponojensis/ monticola 2
antarctica 2
antarctica
antarctica 1
pon./mont. 3
pon./mont. 4a
pon./mont. 4
pon./mont. 4b
sp. 17a
sp. 17
sp. 17b
ponojensis/ monticola 5a
pon./mont. 5b
ponojensis/ monticola 6
ponojensis/ monticola 7
ponojensis/ monticola 8
ponojensis/ monticola 9
pon./mont. 10b
ponojensis/ monticola 10a
1
0.31
0.13
0.43
0.76
0.98
0.002

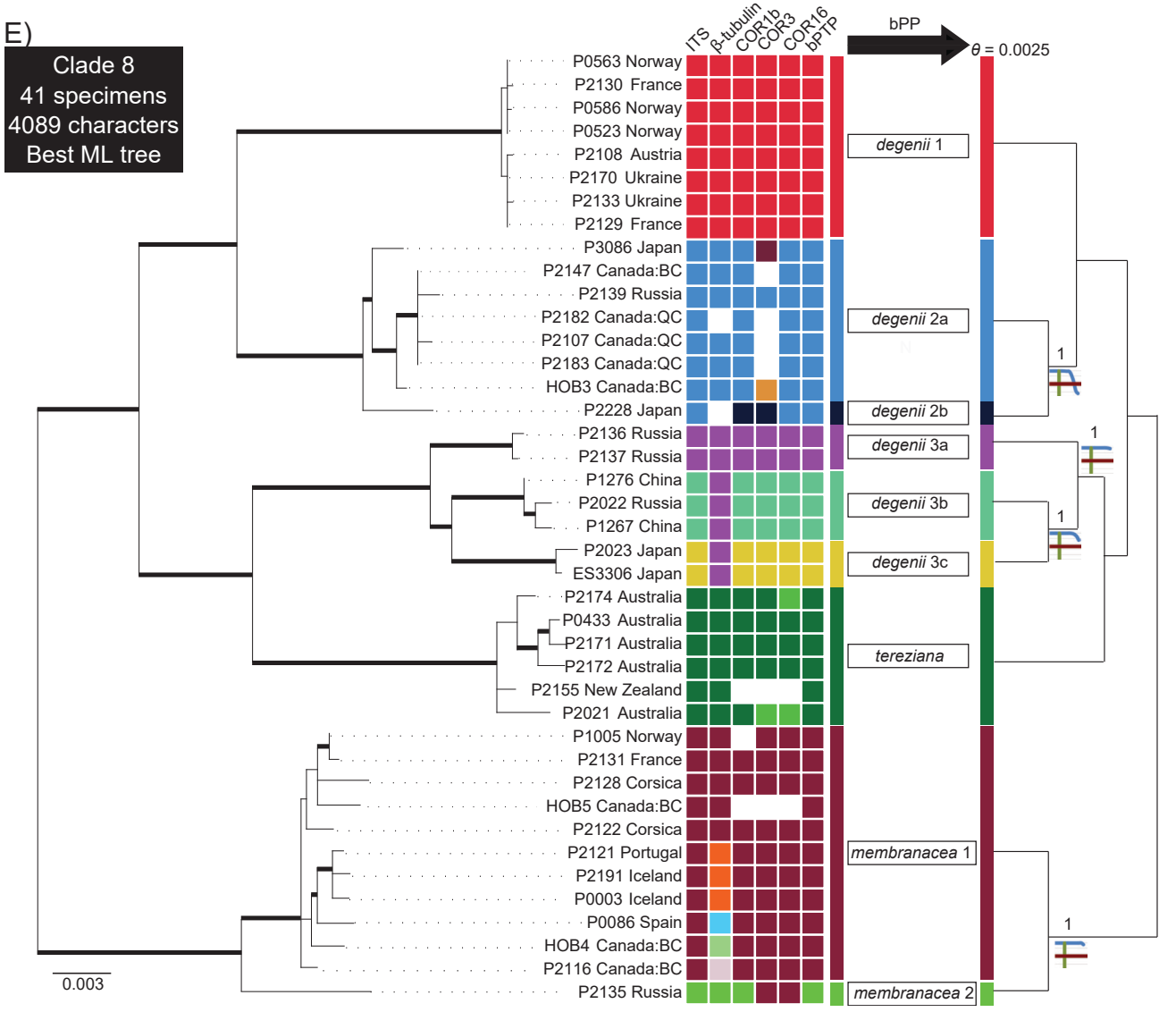
Clade 7. — The *P. cinnamomea* Goward clade includes 23 specimens (Fig. 1) representing three currently recognized species: *P. cinnamomea*, *P. erioderma* Vain., and *P. montis-wilhelmii*, as well as one putative species provisionally named *Peltigera* "*neocanina*" (informally introduced by Miadlikowska & Lutzoni, 2000 and Miadlikowska & al., 2003 and referred to by O'Brien & al., 2009). Discovery analyses on 21 specimens suggested the presence of 8 to 10 species (Fig. 2D; Electr. Suppl.: Table S2). Of the ten lineages representing putative species, bPP validated ($\theta = 0.0032$) all but one (*P.* "*neocanina*" 1a and 1b were merged) (Fig. 2D). *Peltigera* "*neocanina*" seems to include four species, whereas *P. erioderma* and *P. montis-wilhelmi*, each seems to include two distinct species.

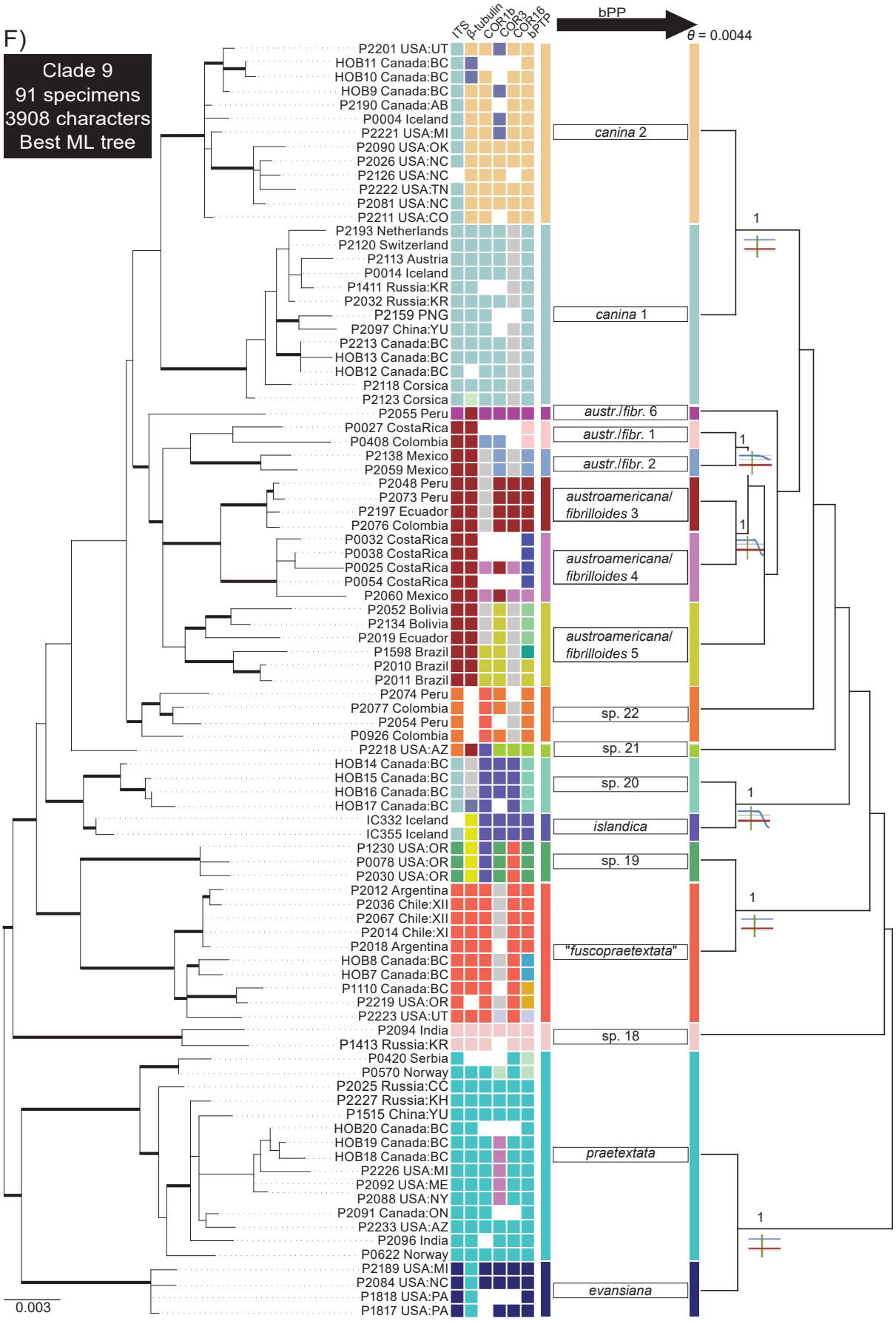
Clade 8. — The *P. degenii*/*P. membranacea* clade includes 42 specimens (Fig. 1) representing three currently recognized species: *P. degenii*, *P. membranacea* and *P. tereziana* Gyeln. Species discovery methods suggested the presence of 8 to 11 species (Fig. 2E; Electr. Suppl.: Table S2). All nine tested lineages representing putative species were validated by bPP ($\theta = 0.0025$) with PP values >0.99 (Fig. 2E). *Peltigera membranacea* and *P. degenii* seem to include two and six species, respectively.

Clade 9. — The *P. canina* clade includes 91 specimens (Fig. 1) representing seven currently recognized species (*P. austroamericana* Zahlbr., *P. canina*, *P. evansiana* Gyeln., *P. fibrilloides* (Gyeln.) Vitik., *P. islandica*, *P. koponenii*, *P. praetextata*), one putative species provisionally named *P.* "*fuscopraetextata*" (informally introduced by Miadlikowska & al. [2003] and referred to by O'Brien & al., 2009) and five unnamed lineages (*Peltigera* spp. 18–22). Species discovery methods showed a high disagreement in the number of suggested putative species




D)
Clade 7
21 specimens
3938 characters
Best ML tree
ITS
β-tubulin
COR1b
COR3
COR16
bPTP
bPP
θ = 0.0032
0.47
1
P0070 USA:NM P2192
USA:AK HOB27
Canada:BC HOB26
Canada:BC P2212
Canada:BC P2098
USA:AK P0068
USA:NM P2202
USA:UT
P2089 USA:CO
P2224 China
P1405 Russia
P2232 Norway
P0006 Iceland HOB21
Canada:BC P2141
Canada HOB23
Canada:BC HOB22
Canada:BC
P2156 Papua New Guinea
P2157 Papua New Guinea
P2162 Papua New Guinea
P2163 Papua New Guinea
"neocanina" 1a
"neocanina" 1
"neocanina" 1b
"neocanina" 2
"neocanina" 3
"neocanina" 4
cinnamomea
montis-wilhelmii1
montis-wilhelmii2
erioderma 1
erioderma 2
0.82
1
0.005


E)
Clade 8
41 specimens
4089 characters
Best ML tree
ITS
β-tubulin
COR1b
COR3
COR16
bPTP
bPP
θ = 0.0025
P0563 Norway
P2130 France
P0586 Norway
P0523 Norway
P2108 Austria
P2170 Ukraine
P2133 Ukraine
P2129 France
P3086 Japan
P2147 Canada:BC
P2139 Russia
P2182 Canada:QC
P2107 Canada:QC
P2183 Canada:QC
HOB3 Canada:BC
P2228 Japan
P2136 Russia
P2137 Russia
P1276 China
P2022 Russia
P1267 China
P2023 Japan
ES3306 Japan
P2174 Australia
P0433 Australia
P2171 Australia
P2172 Australia
P2155 New Zealand
P2021 Australia
P1005 Norway
P2131 France
P2128 Corsica
HOB5 Canada:BC
P2122 Corsica
P2121 Portugal
P2191 Iceland
P0003 Iceland
P0086 Spain
HOB4 Canada:BC
P2116 Canada:BC
P2135 Russia
degenii 1
degenii 2a
degenii 2b
degenii 3a
degenii 3b
degenii 3c
tereziana
membranacea 1
membranacea 2
1
1
1
1
0.003


F)
Clade 9
91 specimens
3908 characters
Best ML tree
ITS
β-tubulin
COR1b
COR3
COR16
bPTP
bPP
θ = 0.0044
P2201 USA:UT
HOB11 Canada:BC
HOB10 Canada:BC
HOB9 Canada:BC
P2190 Canada:AB
P0004 Iceland
P2221 USA:MI
P2090 USA:OK
P2026 USA:NC
P2126 USA:NC
P2222 USA:TN
P2081 USA:NC
P2211 USA:CO
P2193 Netherlands
P2120 Switzerland
P2113 Austria
P0014 Iceland
P1411 Russia:KR
P2032 Russia:KR
P2159 PNG
P2097 China:YU
P2213 Canada:BC
HOB13 Canada:BC
HOB12 Canada:BC
P2118 Corsica
P2123 Corsica
P2055 Peru
P0027 CostaRica
P0408 Colombia
P2138 Mexico
P2059 Mexico
P2048 Peru
P2073 Peru
P2197 Ecuador
P2076 Colombia
P0032 CostaRica
P0038 CostaRica
P0025 CostaRica
P0054 CostaRica
P2060 Mexico
P2052 Bolivia
P2134 Bolivia
P2019 Ecuador
P1598 Brazil
P2010 Brazil
P2011 Brazil
P2074 Peru
P2077 Colombia
P2054 Peru
P0926 Colombia
P2218 USA:AZ
HOB14 Canada:BC
HOB15 Canada:BC
HOB16 Canada:BC
HOB17 Canada:BC
IC332 Iceland
IC355 Iceland
P1230 USA:OR
P0078 USA:OR
P2030 USA:OR
P2012 Argentina
P2036 Chile:XII
P2067 Chile:XII
P2014 Chile:XI
P2018 Argentina
HOB8 Canada:BC
HOB7 Canada:BC
P1110 Canada:BC
P2219 USA:OR
P2223 USA:UT
P2094 India
P1413 Russia:KR
P0420 Serbia
P0570 Norway
P2025 Russia:CC
P2227 Russia:KH
P1515 China:YU
HOB20 Canada:BC
HOB19 Canada:BC
HOB18 Canada:BC
P2226 USA:MI
P2092 USA:ME
P2088 USA:NY
P2091 Canada:ON
P2233 USA:AZ
P2096 India
P0622 Norway
P2189 USA:MI
P2084 USA:NC
P1818 USA:PA
P1817 USA:PA
canina 2
canina 1
austr./fibr. 6
austr./fibr. 1
austr./fibr. 2
austroamericana/ fibrilloides 3
austroamericana/ fibrilloides 4
austroamericana/ fibrilloides 5
sp. 22
sp. 21
sp. 20
islandica
sp. 19
"fuscopraetextata"
sp. 18
praetextata
evansiana
1
1
1
1
1
1
0.003

(10 to 24) and some specimens remained outside of recognized species according to bGMYC (gray boxes in Fig. 2F; Electr. Suppl.: Table S2). Seventeen putative species were subjected to species validation using bPP (θ = 0.0044). All were validated with PP > 0.99. Specimens identified as *Peltigera austroamericana* and *P. fibrilloides* were intermixed within six distinct monophyletic groups (*P. austr./fibr.* 1–6). Monophyletic *Peltigera canina* seems to represent two species, including *Peltigera koponenii* nested in *P. canina* 1. Delimitations of the remaining species, i.e., *P. praetextata*, *P. evansiana*, and *P.* sp. 22 did not change (Fig. 2F).

Contribution of intergenic spacers from COR to species delimitation. — Although species discovery methods provided largely congruent results for most parts of the tree, there were some differences. For example, the addition of the three new COR loci that led to the recognition of a much higher number of species (but see Magain & al., 2017b). Genetic variation in these intergenic spacers could either unveil unknown species diversity not detected by commonly used markers like ITS and β-tubulin, or alternatively could reflect intraspecific structure. Cases supporting the recognition of several lineages deriving exclusively from COR regions include five and six species recognized within *P.* "*neorufescens*" and *P. austroamericana*/*fibrilloides*, respectively, versus 1–2 using other markers (Fig. 2C, F). *Peltigera canina* 1 and 2, which were treated as a single species based on ITS, were resolved as two distinct species based on all other loci, including β-tubulin.

Sensitivity analyses for θ values. — Our species delimitation depends largely on the θ value selected for the bPP validation analyses. It is very difficult to estimate this value because mutation rates and population sizes are unknown for lichen-forming fungi (Magain & al., 2017a). Therefore, we provided information about the observed changes in species delimitation as a function of the θ prior values, to assess the sensitivity of the delimitations and consider alternative hypotheses (Figs. 2A–F; Electr. Suppl.: Table S3). Cases where slightly higher values of θ resulted in the merging of otherwise distinct lineages include *P. ponojensis*/*monticola* 5a and 5b (in clade 5), *P. montis-wilhelmii* 1 and 2 (in clade 7), *P. ulcerata* 1 and 2, and *P. didactyla* 2/*P. sorediifera* (in clade 4). Noticeably higher θ values caused additional merging in *P. islandica* and *Peltigera* sp. 20 in clade 9 (Manoharan-Basil & al., 2016); *P. laciniata* 1 and 2, *P. granulosa* and *P. papuana*, *P.* "*neorufescens*" 1–3, *P. rufescens* 1 and 2 in clade 6, or *P. degenii* 2a and 2b in clade 8. Very high values of θ would lead to much broader species delimitations.

Nucleotide substitution rate heterogeneity among clades 4–7 in section *Peltigera*. — In the five-locus phylogeny (Fig. 1), clade 4 seems to be evolving faster compared to the other clades. We tested various scenarios of rates distribution by enforcing different molecular rate models across a phylogeny resulting from a dataset restricted to clades 4–7. A scenario without molecular clock along the tree (scenario 8; Table 1) was significantly better than the other models. A strict molecular clock (all rates equal, scenario 1) was rejected, suggesting a pattern of rate heterogeneity among clades. A model with a different rate of nucleotide substitution in clade 4 (scenario 2) was the best of the scenarios where a local rate was applied to one specific clade (i.e., compared to scenarios 3–6). A scenario with three rates (one for clade 4, one for clade 5–6 and one for clade 7 (scenario 7), was not significantly better than scenario 2, but was significantly better than the other scenarios with two rates (scenarios 3–6). Our results suggest that the rate of nucleotide substitution in clade 4 (scenario 2) is nearly twice (1.92) as high as in the rest of the tree.

***Nostoc* phylogeny. —** Overall, the *rbcLX* phylogeny with two major *Nostoc* clades and three subclades within *Nostoc* clade 2 (Fig. 3) matches topologies from previous studies (Otálora & al., 2010; Magain & al., 2017a). *Nostoc* clade 1 and subclades 1 and 2 within clade 2 received high support. All cyanobionts associated with members of sections *Peltigera* and *Retifoveatae* belong to *Nostoc* clade 2 subclade 3, and many of them are part of a very large polytomy inside this subclade. In addition to the phylogroups delimited by O'Brien & al. (2013; phylogroups I–VI) and Magain & al. (2017a; phylogroups VII–XX), we recognized 28 phylogroups (phylogroups XXI–XLVIII) to accommodate well-defined clades containing newly added *rbcLX* sequences from *Nostoc* cyanobionts that were not represented in the previous studies. Phylogroups XXV, XXVI, XXVII, XXX, XXXI, XXXII, XXXIII, XXXVII, and XXXIX received low support, however, *Nostoc* strains within many of these clades seem to be associated with *Peltigera* species that share similar ecological conditions. The remaining phylogroups are mostly well-supported by ML bootstrap and/or Bayesian posterior probabilities (Fig. 3).

Specificity of *Peltigera* species. — The Specificity index (S-index) for species of section *Peltigera* ranges from 0.2 to 1 (Electr. Suppl.: Table S5; Figs. 4 and 5). Species for which we obtained *rbcLX* sequences from only three to four thalli show, on average, higher specificity values than species for which we sequenced *rbcLX* from more than four thalli (Fig. 4A). None of these species received an S-index value below 0.4, demonstrating the bias of small sample size toward high levels of specialization. Therefore, we compared the S-index values for species with at least five *rbcLX* sequences. The average specificity is lower in section *Peltigera* (95% confidence interval: 0.49 ± 0.08; Fig. 4B) than in section *Polydactylon* (95% confidence interval: 0.57 ± 0.13; Fig. 4C). Six of 25 species (24%) in section *Peltigera* have S-indexes ≥0.6 (Fig. 4B) compared to 7 of 17 species (41%) in section *Polydactylon* (Fig. 4C); whereas 9 of 25 (36%) species in section *Peltigera* have S-indexes <0.4 versus 5 of 17 (29%) in section *Polydactylon*.

Levels of specificity in section *Peltigera* seem to represent a continuum rather than distinct categories (Fig. 4B). Most species do not show a high degree of specialization, but early diverged species have in general high degrees of specificity (e.g., *P. retifoveata* and its phylogroup XXXIIIa, and *P. kristinssonii* with phylogroup VI [Fig. 5], which is concordant with the study by Magain & al. (2017a) for section *Polydactylon*. However, most early diverged species in section *Peltigera* were generally poorly sampled or are relatively rare, which may partly explain this trend. Moreover, *P. frigida* and *P. aubertii*, part of early speciation events (clades 2a and b), are exceptions with intermediate levels of specialization (Fig. 5).

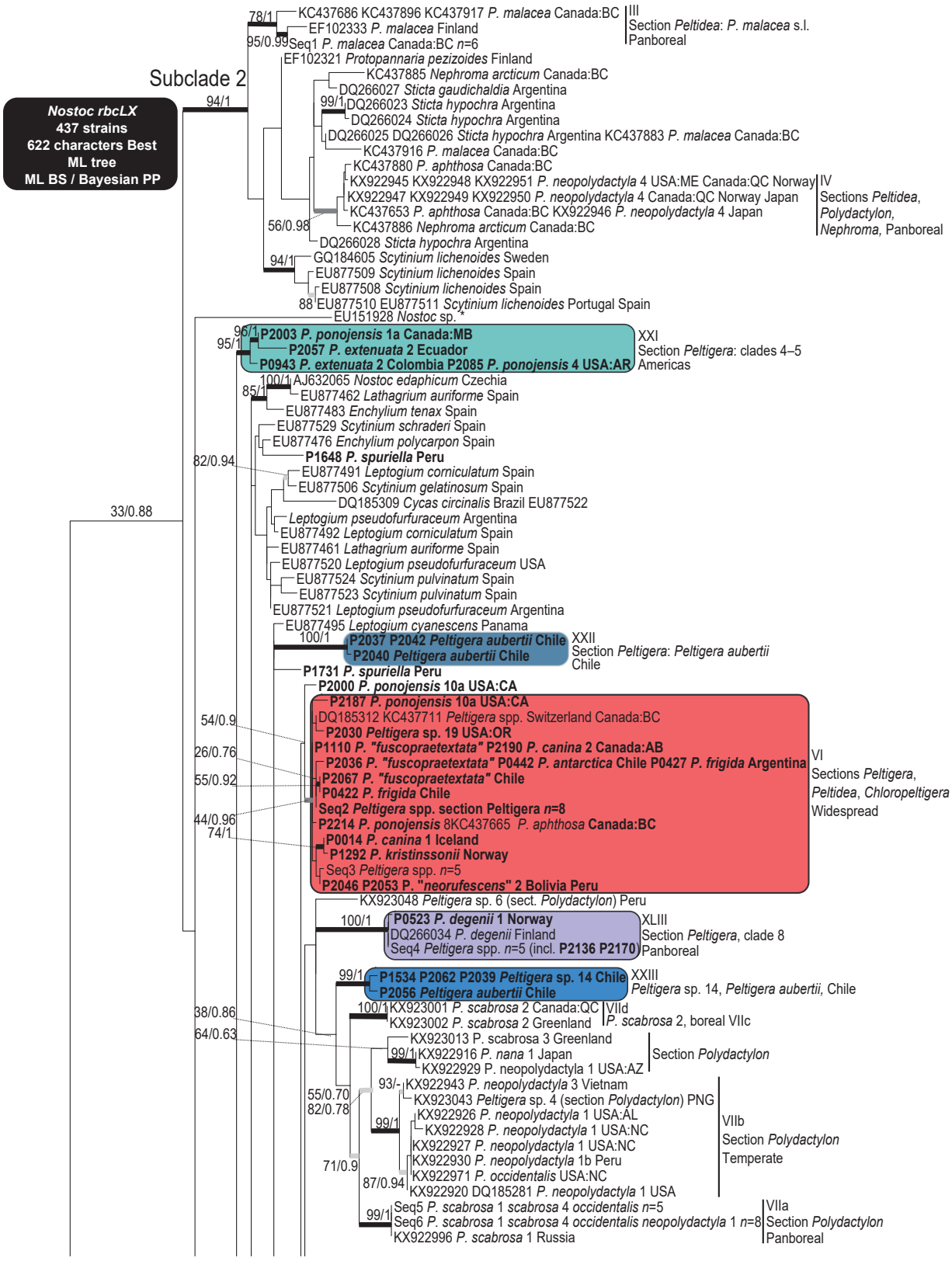
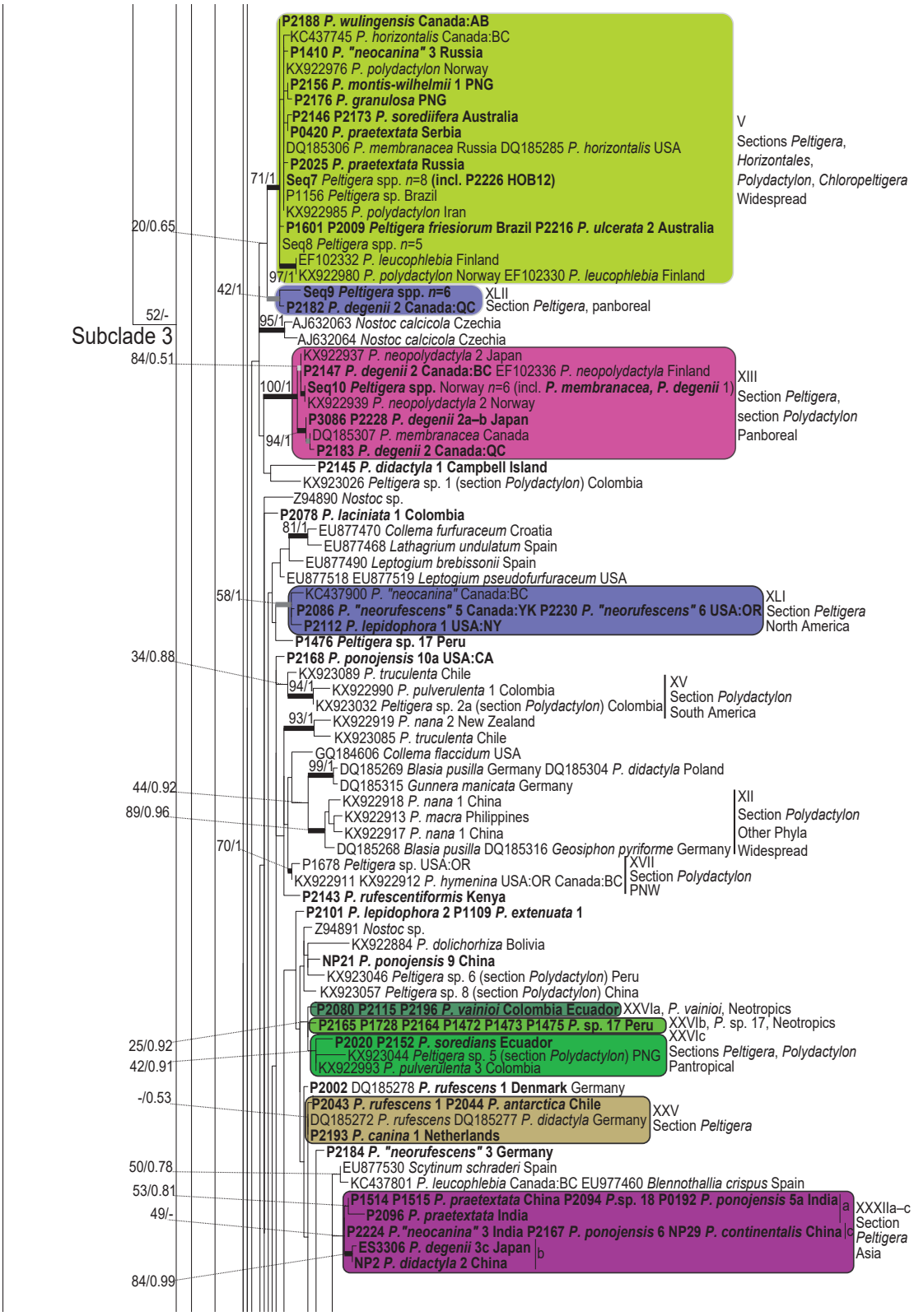
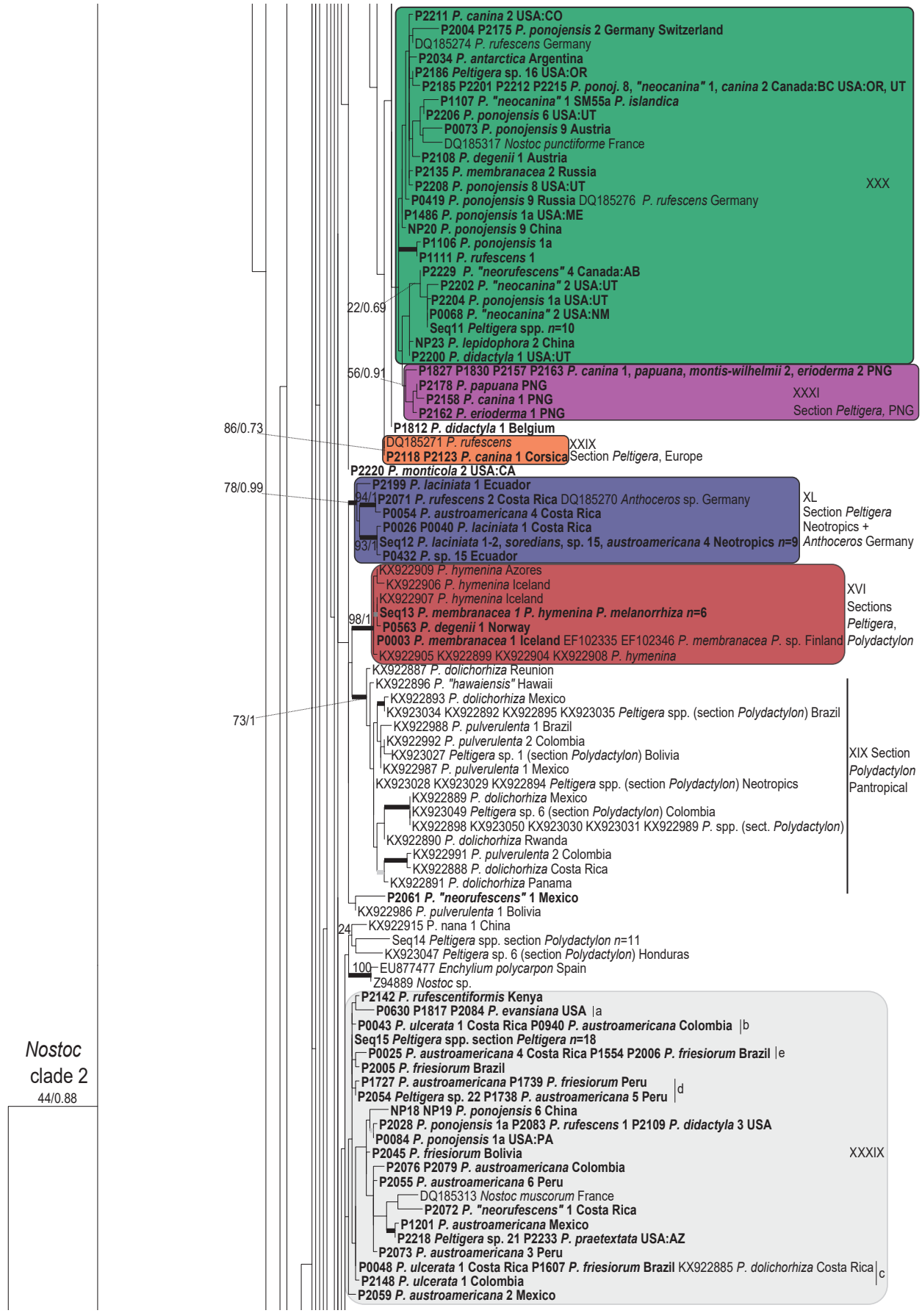
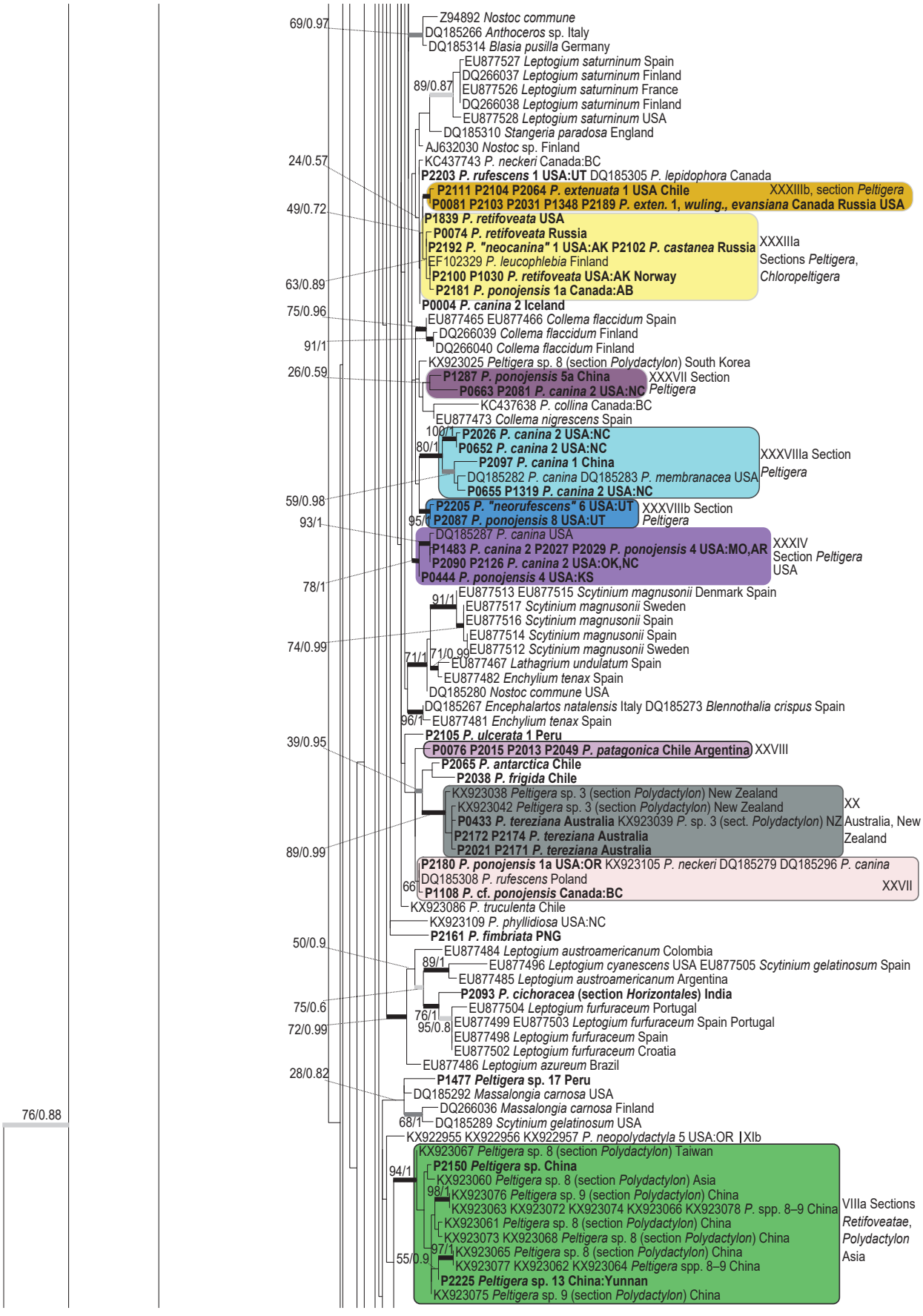


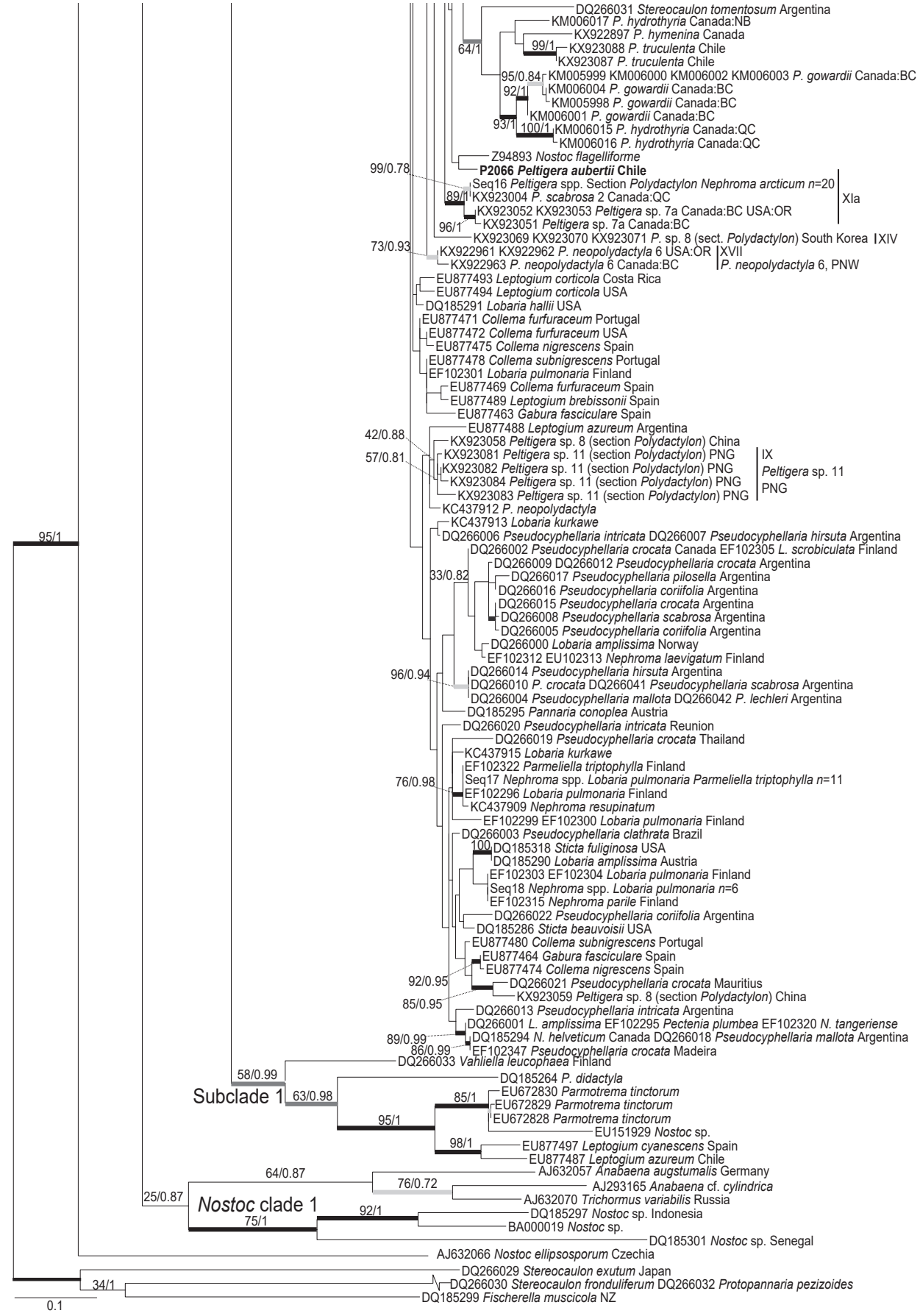
Fig. 3. Best ML tree for *Nostoc* resulting from a phylogenetic analysis on the *rbcLX* locus (622 characters) for 437 strains. The delimitation of *Nostoc* clades and subclades are concordant with Otálora & al. (2010). The delimitation of phylogroups follows O'Brien & al. (2013; phylogroups III–VI), Magain & al. (2017a; phylogroups VII–XX), and this study (phylogroups XXI–XLIII). Strains shown in bold represent sequences from sections *Peltigera* and *Retifoveatae* generated for this study. Colored boxes delimit *Nostoc* phylogroups, which contain newly generated sequences from cyanobionts associated with mycobionts of sections *Peltigera* and *Retifoveatae*. The remaining phylogroups are delimited by ▶



▶ black vertical bars. Values above or below branches represent the ML bootstrap support (before slash) and Bayesian posterior probabilities (after slash) when at least one branch is considered supported (ML BS ≥ 70% and or Bayesian PP ≥ 0.95). Thick branches received ML BS ≥ 70% and Bayesian PP ≥ 0.95, dark gray branches received ML BS < 70% and Bayesian PP ≥ 0.95, whereas light gray branches received ML BS ≥ 70% and Bayesian PP < 0.95. Number of identical sequences (*n*) represented by a single strain in the phylogeny is provided after the terminal name and the complete list of sequences is included in Electr. Suppl.: Table S4. Symbionts of the *ponojensis*/*monticola* clade were abbreviated as *ponojensis* and *austroamericana*/*fibrilloides* as *austroamericana*.


P2211 P. canina 2 USA:CO
P2004 P2175 P. ponojensis 2 Germany Switzerland
DQ185274 P. rufescens Germany
P2034 P. antarctica Argentina
P2186 Peltigera sp. 16 USA:OR
P2185 P2201 P2212 P2215 P. ponoj. 8, "neocanina" 1, canina 2 Canada:BC USA:OR, UT
P1107 P. "neocanina" 1 SM55a P. islandica
P2206 P. ponojensis 6 USA:UT
P0073 P. ponojensis 9 Austria
DQ185317 Nostoc punctiforme France
P2108 P. degenii 1 Austria
P2135 P. membranacea 2 Russia
P2208 P. ponojensis 8 USA:UT
P0419 P. ponojensis 9 Russia DQ185276 P. rufescens Germany
P1486 P. ponojensis 1a USA:ME
NP20 P. ponojensis 9 China
P1106 P. ponojensis 1a
P1111 P. rufescens 1
P2229 P. "neorufescens" 4 Canada:AB
P2202 P. "neocanina" 2 USA:UT
P2204 P. ponojensis 1a USA:UT
P0068 P. "neocanina" 2 USA:NM
Seq11 Peltigera spp. n=10
NP23 P. lepidophora 2 China
P2200 P. didactyla 1 USA:UT
XXX
22/0.69
56/0.91
P1827 P1830 P2157 P2163 P. canina 1, papuana, montis-wilhelmii 2, erioderma 2 PNG
P2178 P. papuana PNG
P2158 P. canina 1 PNG
P2162 P. erioderma 1 PNG
XXXI
Section Peltigera, PNG
86/0.73
P1812 P. didactyla 1 Belgium
DQ185271 P. rufescens
P2118 P2123 P. canina 1 Corsica
XXIX
Section Peltigera, Europe
P2220 P. monticola 2 USA:CA
78/0.99
P2199 P. laciniata 1 Ecuador
94/1
P2071 P. rufescens 2 Costa Rica DQ185270 Anthoceros sp. Germany
P0054 P. austroamericana 4 Costa Rica
P0026 P0040 P. laciniata 1 Costa Rica
93/1
Seq12 P. laciniata 1-2, soredians, sp. 15, austroamericana 4 Neotropics n=9
P0432 P. sp. 15 Ecuador
XL
Section Peltigera
Neotropics +
Anthoceros Germany
KX922909 P. hymenina Azores
KX922906 P. hymenina Iceland
KX922907 P. hymenina Iceland
98/1
Seq13 P. membranacea 1 P. hymenina P. melanorrhiza n=6
P0563 P. degenii 1 Norway
P0003 P. membranacea 1 Iceland EF102335 EF102346 P. membranacea P. sp. Finland
KX922905 KX922899 KX922904 KX922908 P. hymenina
XVI
Sections
Peltigera,
Polydactylon
KX922887 P. dolichorhiza Reunion
KX922896 P. "hawaiensis" Hawaii
KX922893 P. dolichorhiza Mexico
73/1
KX923034 KX922892 KX922895 KX923035 Peltigera spp. (section Polydactylon) Brazil
KX922988 P. pulverulenta 1 Brazil
KX922992 P. pulverulenta 2 Colombia
KX923027 Peltigera sp. 1 (section Polydactylon) Bolivia
KX922987 P. pulverulenta 1 Mexico
KX923028 KX923029 KX922894 Peltigera spp. (section Polydactylon) Neotropics
KX922889 P. dolichorhiza Mexico
KX923049 Peltigera sp. 6 (section Polydactylon) Colombia
KX922898 KX923050 KX923030 KX923031 KX922989 P. spp. (sect. Polydactylon)
KX922890 P. dolichorhiza Rwanda
KX922991 P. pulverulenta 2 Colombia
KX922888 P. dolichorhiza Costa Rica
KX922891 P. dolichorhiza Panama
XIX Section
Polydactylon
Pantropical
P2061 P. "neorufescens" 1 Mexico
KX922986 P. pulverulenta 1 Bolivia
24
KX922915 P. nana 1 China
Seq14 Peltigera spp. section Polydactylon n=11
KX923047 Peltigera sp. 6 (section Polydactylon) Honduras
100
EU877477 Enchylium polycarpon Spain
Z94889 Nostoc sp.
Nostoc
clade 2
44/0.88
P2142 P. rufescentiformis Kenya
P0630 P1817 P2084 P. evansiana USA
a
P0043 P. ulcerata 1 Costa Rica P0940 P. austroamericana Colombia
b
Seq15 Peltigera spp. section Peltigera n=18
P0025 P. austroamericana 4 Costa Rica P1554 P2006 P. friesiorum Brazil
e
P2005 P. friesiorum Brazil
P1727 P. austroamericana P1739 P. friesiorum Peru
d
P2054 Peltigera sp. 22 P1738 P. austroamericana 5 Peru
NP18 NP19 P. ponojensis 6 China
P2028 P. ponojensis 1a P2083 P. rufescens 1 P2109 P. didactyla 3 USA
P0084 P. ponojensis 1a USA:PA
P2045 P. friesiorum Bolivia
XXXIX
P2076 P2079 P. austroamericana Colombia
P2055 P. austroamericana 6 Peru
DQ185313 Nostoc muscorum France
P2072 P. "neorufescens" 1 Costa Rica
P1201 P. austroamericana Mexico
P2218 Peltigera sp. 21 P2233 P. praetextata USA:AZ
P2073 P. austroamericana 3 Peru
P0048 P. ulcerata 1 Costa Rica P1607 P. friesiorum Brazil KX922885 P. dolichorhiza Costa Rica
c
P2148 P. ulcerata 1 Colombia
P2059 P. austroamericana 2 Mexico


Z94892 Nostoc commune
DQ185266 Anthoceros sp. Italy
DQ185314 Blasia pusilla Germany
EU877527 Leptogium saturninum Spain
DQ266037 Leptogium saturninum Finland
EU877526 Leptogium saturninum France
DQ266038 Leptogium saturninum Finland
EU877528 Leptogium saturninum USA
DQ185310 Stangeria paradosa England
AJ632030 Nostoc sp. Finland
KC437743 P. neckeri Canada:BC
P2203 P. rufescens 1 USA:UT DQ185305 P. lepidophora Canada
P2111 P2104 P2064 P. extenuata 1 USA Chile
P0081 P2103 P2031 P1348 P2189 P. exten. 1, wuling., evansiana Canada Russia USA
XXXIIIb, section Peltigera
P1839 P. retifoveata USA
P0074 P. retifoveata Russia
P2192 P. "neocanina" 1 USA:AK P2102 P. castanea Russia
EF102329 P. leucophlebia Finland
P2100 P1030 P. retifoveata USA:AK Norway
P2181 P. ponojensis 1a Canada:AB
XXXIIIa Sections Peltigera, Chloropeltigera
P0004 P. canina 2 Iceland
EU877465 EU877466 Collema flaccidum Spain
DQ266039 Collema flaccidum Finland
DQ266040 Collema flaccidum Finland
KX923025 Peltigera sp. 8 (section Polydactylon) South Korea
P1287 P. ponojensis 5a China
P0663 P2081 P. canina 2 USA:NC
XXXVII Section Peltigera
KC437638 P. collina Canada:BC
EU877473 Collema nigrescens Spain
P2026 P. canina 2 USA:NC
P0652 P. canina 2 USA:NC
P2097 P. canina 1 China
DQ185282 P. canina DQ185283 P. membranacea USA
P0655 P1319 P. canina 2 USA:NC
XXXVIIIa Section Peltigera
P2205 P. "neorufescens" 6 USA:UT
P2087 P. ponojensis 8 USA:UT
XXXVIIIb Section Peltigera
DQ185287 P. canina USA
P1483 P. canina 2 P2027 P2029 P. ponojensis 4 USA:MO,AR
P2090 P2126 P. canina 2 USA:OK,NC
P0444 P. ponojensis 4 USA:KS
XXXIV Section Peltigera USA
EU877513 EU877515 Scytinium magnusonii Denmark Spain
EU877517 Scytinium magnusonii Sweden
EU877516 Scytinium magnusonii Spain
EU877514 Scytinium magnusonii Spain
EU877512 Scytinium magnusonii Sweden
EU877467 Lathagrium undulatum Spain
EU877482 Enchylium tenax Spain
DQ185280 Nostoc commune USA
DQ185267 Encephalartos natalensis Italy DQ185273 Blennothalia crispus Spain
EU877481 Enchylium tenax Spain
P2105 P. ulcerata 1 Peru
P0076 P2015 P2013 P2049 P. patagonica Chile Argentina
XXVIII
P2065 P. antarctica Chile
P2038 P. frigida Chile
KX923038 Peltigera sp. 3 (section Polydactylon) New Zealand
KX923042 Peltigera sp. 3 (section Polydactylon) New Zealand
P0433 P. tereziana Australia KX923039 P. sp. 3 (sect. Polydactylon) NZ
P2172 P2174 P. tereziana Australia
P2021 P2171 P. tereziana Australia
XX Australia, New Zealand
P2180 P. ponojensis 1a USA:OR KX923105 P. neckeri DQ185279 DQ185296 P. canina
DQ185308 P. rufescens Poland
P1108 P. cf. ponojensis Canada:BC
XXVII
KX923086 P. truculenta Chile
KX923109 P. phyllidiosa USA:NC
P2161 P. fimbriata PNG
EU877484 Leptogium austroamericanum Colombia
EU877496 Leptogium cyanescens USA EU877505 Scytinium gelatinosum Spain
EU877485 Leptogium austroamericanum Argentina
P2093 P. cichoracea (section Horizontales) India
EU877504 Leptogium furfuraceum Portugal
EU877499 EU877503 Leptogium furfuraceum Spain Portugal
EU877498 Leptogium furfuraceum Spain
EU877502 Leptogium furfuraceum Croatia
EU877486 Leptogium azureum Brazil
P1477 Peltigera sp. 17 Peru
DQ185292 Massalongia carnosa USA
DQ266036 Massalongia carnosa Finland
DQ185289 Scytinium gelatinosum USA
KX922955 KX922956 KX922957 P. neopolydactyla 5 USA:OR
XIb
KX923067 Peltigera sp. 8 (section Polydactylon) Taiwan
P2150 Peltigera sp. China
KX923060 Peltigera sp. 8 (section Polydactylon) Asia
KX923076 Peltigera sp. 9 (section Polydactylon) China
KX923063 KX923072 KX923074 KX923066 KX923078 P. spp. 8–9 China
KX923061 Peltigera sp. 8 (section Polydactylon) China
KX923073 KX923068 Peltigera sp. 8 (section Polydactylon) China
KX923065 Peltigera sp. 8 (section Polydactylon) China
KX923077 KX923062 KX923064 Peltigera spp. 8–9 China
P2225 Peltigera sp. 13 China:Yunnan
KX923075 Peltigera sp. 9 (section Polydactylon) China
VIIIa Sections Retifoveatae, Polydactylon Asia
69/0.97
89/0.87
24/0.57
49/0.72
63/0.89
75/0.96
91/1
26/0.59
100/1
80/1
59/0.98
95/1
93/1
78/1
91/1
74/0.99
71/1
71/0.99
96/1
39/0.95
89/0.99
66
50/0.9
89/1
75/0.6
76/1
72/0.99
95/0.8
28/0.82
76/0.88
68/1
94/1
98/1
97/1
55/0.9


DQ266031 Stereocaulon tomentosum Argentina
KM006017 P. hydrothyria Canada:NB
KX922897 P. hymenina Canada
64/1
99/1
KX923088 P. truculenta Chile
KX923087 P. truculenta Chile
95/0.84
KM005999 KM006000 KM006002 KM006003 P. gowardii Canada:BC
92/1
KM006004 P. gowardii Canada:BC
KM005998 P. gowardii Canada:BC
93/1
KM006001 P. gowardii Canada:BC
100/1
KM006015 P. hydrothyria Canada:QC
KM006016 P. hydrothyria Canada:QC
Z94893 Nostoc flagelliforme
99/0.78
P2066 Peltigera aubertii Chile
Seq16 Peltigera spp. Section Polydactylon Nephroma arcticum n=20
89/1
KX923004 P. scabrosa 2 Canada:QC
KX923052 KX923053 Peltigera sp. 7a Canada:BC USA:OR
XIa
96/1
KX923051 Peltigera sp. 7a Canada:BC
KX923069 KX923070 KX923071 P. sp. 8 (sect. Polydactylon) South Korea
XIV
73/0.93
KX922961 KX922962 P. neopolydactyla 6 USA:OR
XVII
KX922963 P. neopolydactyla 6 Canada:BC
P. neopolydactyla 6, PNW
EU877493 Leptogium corticola Costa Rica
EU877494 Leptogium corticola USA
DQ185291 Lobaria hallii USA
EU877471 Collema furfuraceum Portugal
EU877472 Collema furfuraceum USA
EU877475 Collema nigrescens Spain
EU877478 Collema subnigrescens Portugal
EF102301 Lobaria pulmonaria Finland
EU877469 Collema furfuraceum Spain
EU877489 Leptogium brebissonii Spain
EU877463 Gabura fasciculare Spain
EU877488 Leptogium azureum Argentina
42/0.88
KX923058 Peltigera sp. 8 (section Polydactylon) China
57/0.81
KX923081 Peltigera sp. 11 (section Polydactylon) PNG
IX
KX923082 Peltigera sp. 11 (section Polydactylon) PNG
Peltigera sp. 11
KX923084 Peltigera sp. 11 (section Polydactylon) PNG
PNG
KX923083 Peltigera sp. 11 (section Polydactylon) PNG
KC437912 P. neopolydactyla
KC437913 Lobaria kurkawe
95/1
DQ266006 Pseudocyphellaria intricata DQ266007 Pseudocyphellaria hirsuta Argentina
DQ266002 Pseudocyphellaria crocata Canada EF102305 L. scrobiculata Finland
DQ266009 DQ266012 Pseudocyphellaria crocata Argentina
33/0.82
DQ266017 Pseudocyphellaria pilosella Argentina
DQ266016 Pseudocyphellaria coriifolia Argentina
DQ266015 Pseudocyphellaria crocata Argentina
DQ266008 Pseudocyphellaria scabrosa Argentina
DQ266005 Pseudocyphellaria coriifolia Argentina
DQ266000 Lobaria amplissima Norway
EF102312 EU102313 Nephroma laevigatum Finland
96/0.94
DQ266014 Pseudocyphellaria hirsuta Argentina
DQ266010 P. crocata DQ266041 Pseudocyphellaria scabrosa Argentina
DQ266004 Pseudocyphellaria mallota DQ266042 P. lechleri Argentina
DQ185295 Pannaria conoplea Austria
DQ266020 Pseudocyphellaria intricata Reunion
DQ266019 Pseudocyphellaria crocata Thailand
KC437915 Lobaria kurkawe
EF102322 Parmeliella triptophylla Finland
76/0.98
Seq17 Nephroma spp. Lobaria pulmonaria Parmeliella triptophylla n=11
EF102296 Lobaria pulmonaria Finland
KC437909 Nephroma resupinatum
EF102299 EF102300 Lobaria pulmonaria Finland
DQ266003 Pseudocyphellaria clathrata Brazil
100
DQ185318 Sticta fuliginosa USA
DQ185290 Lobaria amplissima Austria
EF102303 EF102304 Lobaria pulmonaria Finland
Seq18 Nephroma spp. Lobaria pulmonaria n=6
EF102315 Nephroma parile Finland
DQ266022 Pseudocyphellaria coriifolia Argentina
DQ185286 Sticta beauvoisii USA
EU877480 Collema subnigrescens Portugal
EU877464 Gabura fasciculare Spain
EU877474 Collema nigrescens Spain
92/0.95
DQ266021 Pseudocyphellaria crocata Mauritius
KX923059 Peltigera sp. 8 (section Polydactylon) China
85/0.95
DQ266013 Pseudocyphellaria intricata Argentina
DQ266001 L. amplissima EF102295 Pectenia plumbea EF102320 N. tangeriense
89/0.99
DQ185294 N. helveticum Canada DQ266018 Pseudocyphellaria mallota Argentina
86/0.99
EF102347 Pseudocyphellaria crocata Madeira
DQ266033 Vahliella leucophaea Finland
58/0.99
DQ185264 P. didactyla
Subclade 1
63/0.98
85/1
EU672830 Parmotrema tinctorum
EU672829 Parmotrema tinctorum
95/1
EU672828 Parmotrema tinctorum
EU151929 Nostoc sp.
98/1
EU877497 Leptogium cyanescens Spain
EU877487 Leptogium azureum Chile
64/0.87
AJ632057 Anabaena augstumalis Germany
76/0.72
AJ293165 Anabaena cf. cylindrica
25/0.87
AJ632070 Trichormus variabilis Russia
Nostoc clade 1
92/1
75/1
DQ185297 Nostoc sp. Indonesia
BA000019 Nostoc sp.
DQ185301 Nostoc sp. Senegal
AJ632066 Nostoc ellipsosporum Czechia
DQ266029 Stereocaulon exutum Japan
34/1
DQ266030 Stereocaulon fronduliferum DQ266032 Protopannaria pezizoides
DQ185299 Fischerella muscicola NZ
0.1

Contrary to the recent neotropical species of section *Polydactylon*, which are mostly generalists (Magain & al., 2017a), neotropical species from section *Peltigera* displayed moderate to high levels of specificity toward their cyanobionts, except for *P. friesiorum* with a Specificity index of 0.36 (Fig. 5). In section *Peltigera*, we detected two examples of one-to-one reciprocal specificity: *P. vainioi* with its phylogroup XXVIa and *P. patagonica* with phylogroup XXVIII. Another example of strong specificity involves the widespread *P. extenuata* 1, which was found with phylogroup XXXIIIb along a broad geographic range from Chile to Russia (Krasnoyarsk Region).

Distribution and specificity of *Nostoc* phylogroups. — Many *Nostoc* phylogroups associating with members of section *Peltigera* are widespread geographically and were found in association with multiple *Peltigera* species from this section. For example, phylogroup V occurred in 53 thalli of 20 species from section *Peltigera* (clades 4–9; Fig. 5). This *Nostoc* phylogroup was found in association with five species from section *Polydactylon*, and members of three other sections (*P.* sect. *Horizontales* Miądl. & Lutzoni, sect. *Peltidea*, sect. *Chloropeltigera*; Magain & al., 2017a). *Nostoc* phylogroup V has an almost cosmopolitan distribution and was collected on all continents except Africa and Antarctica, from where little or no data is available (Fig. 3). *Nostoc* phylogroup VI was found in 28 thalli representing 12 species from four clades of section *Peltigera* (Fig. 5). This phylogroup is also commonly associated with species from section *Chloropeltigera* (Fig. 3) (O'Brien & al., 2013; Magain & al., 2017a; Pardo-De la Hoz & al., in press) and was collected in the two Americas and in Europe. Phylogroup XXX was reported from 35 thalli representing 19 species, whereas phylogroup XXXIX was found in 36 thalli

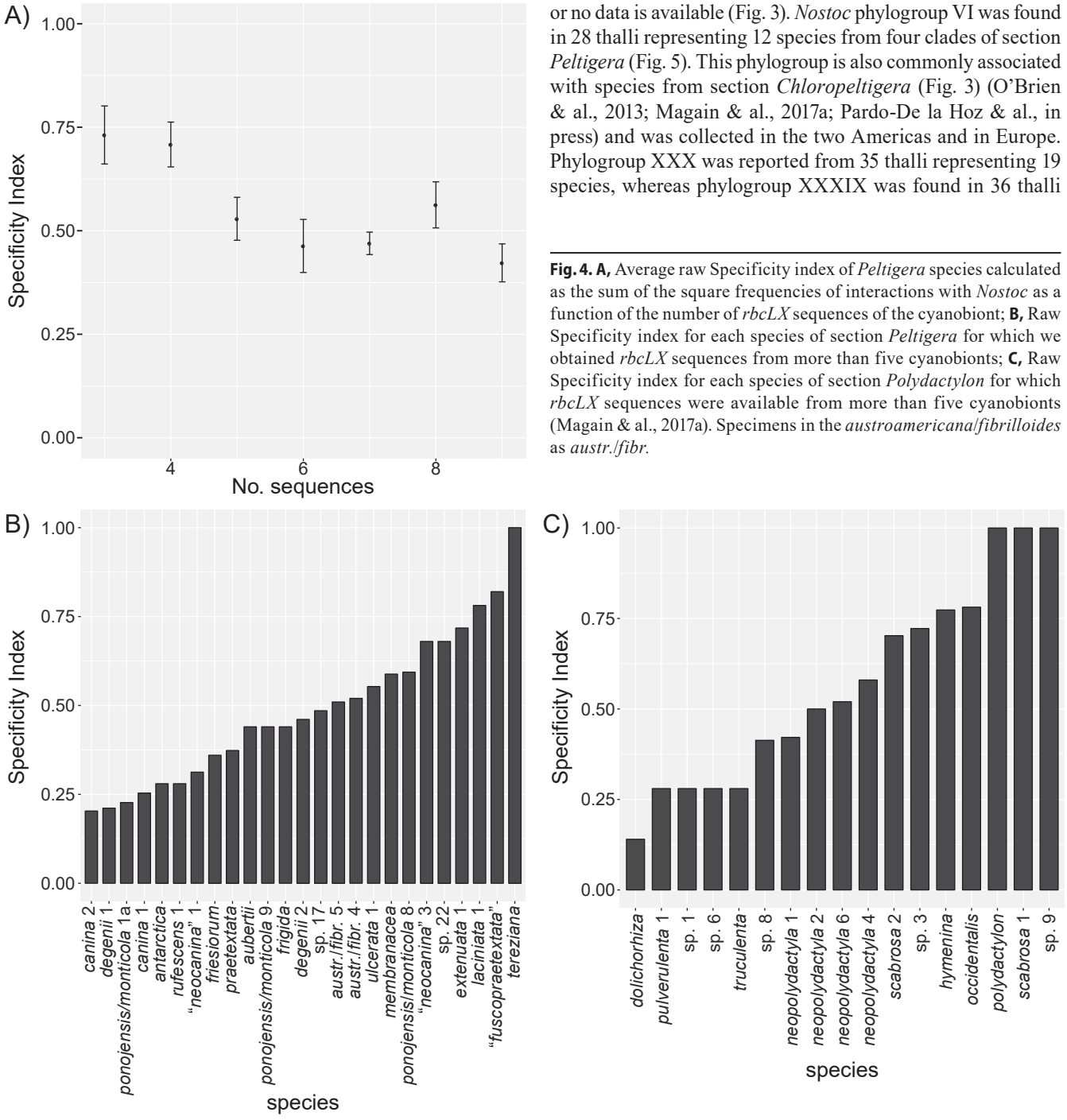


Fig. 4. A, Average raw Specificity index of *Peltigera* species calculated as the sum of the square frequencies of interactions with *Nostoc* as a function of the number of *rbcLX* sequences of the cyanobiont; **B,** Raw Specificity index for each species of section *Peltigera* for which we obtained *rbcLX* sequences from more than five cyanobionts; **C,** Raw Specificity index for each species of section *Polydactylon* for which *rbcLX* sequences were available from more than five cyanobionts (Magain & al., 2017a). Specimens in the *austroamericana*/*fibrilloides* as *austr./fibr.*

Table 2. Likelihood values and estimations of parameters for the six models tested for biogeographical analyses with BioGeoBEARS.

Model	LnL	No. parameters	d	e	j
DEC	−331.5867	2	0.0610	0.0425	0
DEC+J	**−305.2048**	3	0.0437	1.00E-12	0.0433
DIVALIKE	−327.2447	2	0.0688	1.00E-12	0
DIVALIKE+J	−309.0618	3	0.0504	1.38E-08	0.0341
BAYAREALIKE	−352.1448	2	0.0594	0.6401	0
BAYAREALIKE+J	−315.6641	3	0.0355	1.00E-07	0.0676

The best likelihood value is shown in bold. d, dispersal; e, local extinction; j, founder effect.

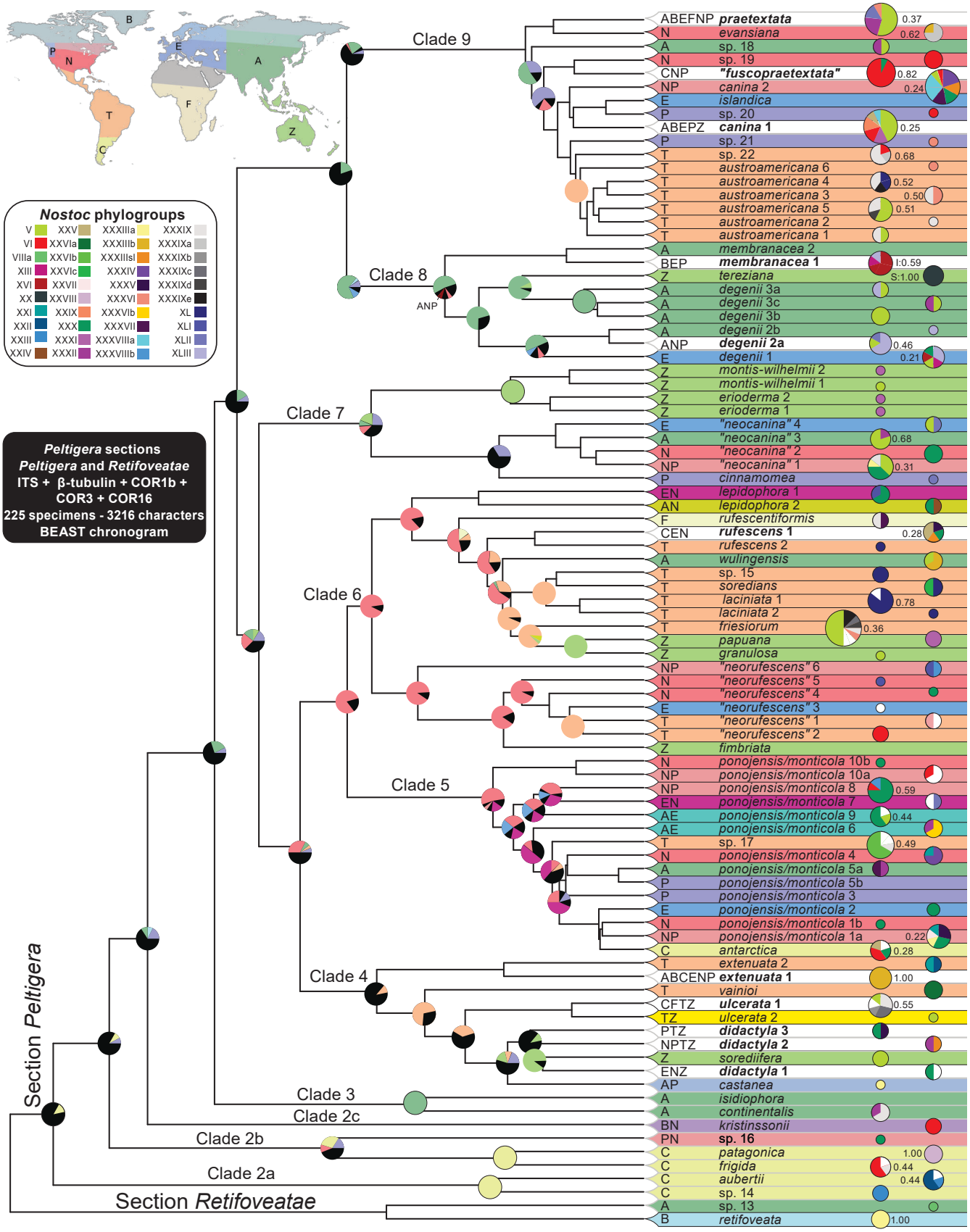
representing 14 species (Fig. 5). These two phylogroups have almost cosmopolitan distributions. However, their monophyletic delimitation was poorly supported in the *Nostoc* phylogeny (Fig. 3).

Similar to other sections such as *Peltidea* and *Polydactylon* (O'Brien & al., 2013; Magain & al., 2017a), *Nostoc* phylogroups with very high specificity were also found in section *Peltigera*. They involve three phylogroups from the Neantarctic region: phylogroup XXII associated exclusively with *Peltigera aubertii*, phylogroup XXVIII found with *P. patagonica*, and phylogroup XXIII associated with *Peltigera* sp. 14 and a single specimen of *Peltigera aubertii*. Cases of high *Nostoc* phylogroup specificity were also found in the Neotropics: phylogroup XXVIa was found only from thalli of *P. vainioi*, and phylogroup XXVIb from *P.* sp. 17. Some other phylogroups were restricted to a single region, for example phylogroup XXXI did not occur outside of Papua New Guinea (Fig. 3).

Nostoc phylogroup specificity was also detected at broader phylogenetic scales. For example, some *Nostoc* phylogroups are currently known to associate with only one section of the genus *Peltigera*. Nineteen *Nostoc* phylogroups were found exclusively in association with *Peltigera* species from sections *Peltigera* and *Retifoveatae*. Fourteen phylogroups associating with species from section *Polydactylon* were never found in thalli of *Peltigera* species from section *Peltigera* (Fig. 3; Magain & al., 2017a). This broader phylogenetic scale of specificity does not pertain only to rare phylogroups. Very common phylogroups in section *Polydactylon* (e.g., VIIa, VIIb, XIa, and IV) have not yet been recovered from thalli of species from section *Peltigera*. Similarly, phylogroups VI, XXX and XXXIX, commonly found in section *Peltigera*, seemingly do not form symbiotic associations with *Peltigera* species from section *Polydactylon*. The only phylogroups shared by sections *Peltigera*, *Retifoveatae* and *Polydactylon* are phylogroups V, VIIIa, XIII, XVI and XX (Fig. 3).

Biogeographical history of *Peltigera* section *Peltigera*. — The DEC+J model has three parameters: dispersal (d), local extinction (e) and founder-effect (j) (Table 2). In our BioGeoBears analysis, the local extinction (e) parameter was close to 0, whereas we obtained similar values (~0.043) for parameters d and j. All three models with parameter j (Table 2), as well as DIVALIKE estimated very low values for the local extinction parameter (e), whereas values of d and e were of the same order for the DEC and BAYAREALIKE models. Under the DEC+J model, the ancestor of section *Peltigera* originated in the Neantarctic region, but several subsequent nodes were reconstructed as of Asian origin, including the common ancestor of clades 8 and 9. The ancestors of clades 5–7 most likely inhabited North America, and the ancestor of clade 4 the Neotropics.

Fig. 5. Biogeographical patterns and specificity of *Peltigera* species within sections *Peltigera* and *Retifoveatae* toward their cyanobiont. The main tree represents a simplified BEAST chronogram (five-locus tree based on 3216 characters for 225 specimens) where each of the 90 putative *Peltigera* species from sections *Peltigera* and *Retifoveatae*, as defined by species delimitation methods (Fig. 2), is represented by one terminal branch. Pie charts associated with selected nodes summarize results of the biogeographical ancestral analysis as implemented in BioGeoBEARS, using the DEC+J model (Table 2). Pie charts color scheme corresponds to areas delimited in the map on the top left corner and black color represents the sum of all remaining probabilities. Background colors extending from the terminal branches and corresponding abbreviations represent geographic regions where thalli were sampled (as shown on the map on the top left corner). Additional colors are used when the species is present in two regions. Those correspond to their two-letter codes. When a species was collected in three or more regions, the name of the species is shown in bold and the background color is white. The capital letters in front of the species epithet refer to the capital letters on the geographical map: A = Asia, B = Panboreal, C = Neantarctics, E = Europe, F = Africa, N = North America, P = Pacific Northwest, T = Neotropics, Z = Australasia. The pie charts on the right of the species epithets represent the *Nostoc* phylogroups with which each species is associated. The size of each pie chart is proportional to the number of *rbcLX* sequences available for this species and the sizes of the portions within each pie chart correspond to the number of *rbcLX* sequences representing each phylogroup. Species for which we have no *Nostoc* information do not have a pie chart. The colors within pie charts correspond to *Nostoc* phylogroups as defined in Fig. 3 and represented in the legend provided here. White portions of the pie charts represent *Nostoc* haplotypes that are outside of defined phylogroups. When four or more *rbcLX* sequences were available, the raw Specificity index is shown next to the corresponding pie chart. Specimens in the *austroamericana*/*fibrilloides* as *austroamericana*.


B
P
N
E
A
F
T
Z
C
Nostoc phylogroups
V XXV XXXIIIa XXXIX
VI XXVIa XXXIIIb XXXIXa
VIIIa XXVIb XXXIIIsl XXXIXb
XIII XXVIc XXXIV XXXIXc
XVI XXVII XXXV XXXIXd
XX XXVIII XXXVI XXXIXe
XXI XXIX XXXVIb XL
XXII XXX XXXVII XLI
XXIII XXXI XXXVIIIa XLII
XXIV XXXII XXXVIIIb XLIII
Peltigera sections Peltigera and Retifoveatae
ITS + β-tubulin + COR1b + COR3 + COR16
225 specimens - 3216 characters
BEAST chronogram
Clade 9
Clade 8
ANP
Clade 7
Clade 6
Clade 5
Clade 4
Clade 3
Clade 2c
Clade 2b
Clade 2a
Section Peltigera
Section Retifoveatae
ABEFNP praetextata 0.37
N evansiana 0.62
A sp. 18
N sp. 19
CNP "fuscopraetextata" 0.82
NP canina 2 0.24
E islandica
P sp. 20
ABEPZ canina 1 0.25
P sp. 21
T sp. 22 0.68
T austroamericana 6
T austroamericana 4 0.52
T austroamericana 3 0.50
T austroamericana 5 0.51
T austroamericana 2
T austroamericana 1
A membranacea 2
BEP membranacea 1 I:0.59
Z tereziana S:1.00
A degenii 3a
A degenii 3c
A degenii 3b
A degenii 2b
ANP degenii 2a 0.46
E degenii 1 0.21
Z montis-wilhelmii 2
Z montis-wilhelmii 1
Z erioderma 2
Z erioderma 1
E "neocanina" 4
A "neocanina" 3 0.68
N "neocanina" 2
NP "neocanina" 1 0.31
P cinnamomea
EN lepidophora 1
AN lepidophora 2
F rufescentiformis
CEN rufescens 1 0.28
T rufescens 2
A wulingensis
T sp. 15
T soredians
T laciniata 1 0.78
T laciniata 2
T friesiorum 0.36
Z papuana
Z granulosa
NP "neorufescens" 6
N "neorufescens" 5
N "neorufescens" 4
E "neorufescens" 3
T "neorufescens" 1
T "neorufescens" 2
Z fimbriata
N ponojensis/monticola 10b
NP ponojensis/monticola 10a
NP ponojensis/monticola 8 0.59
EN ponojensis/monticola 7
AE ponojensis/monticola 9 0.44
AE ponojensis/monticola 6
T sp. 17 0.49
N ponojensis/monticola 4
A ponojensis/monticola 5a
P ponojensis/monticola 5b
P ponojensis/monticola 3
E ponojensis/monticola 2
N ponojensis/monticola 1b
NP ponojensis/monticola 1a 0.22
C antarctica 0.28
T extenuata 2
ABCENP extenuata 1 1.00
T vainioi
CFTZ ulcerata 1 0.55
TZ ulcerata 2
PTZ didactyla 3
NPTZ didactyla 2
Z sorediifera
ENZ didactyla 1
AP castanea
A isidiophora
A continentalis
BN kristinssonii
PN sp. 16
C patagonica 1.00
C frigida 0.44
C aubertii 0.44
C sp. 14
A sp. 13
B retifoveata 1.00

ITS1 hypervariable region (ITS1-HR) sequence comparison. — A high level of variation among ITS sequences especially within the ITS1 spacer, required the exclusion of 50% of the total 1036 sites of the alignment used for phylogenetic analyses. One of the excluded ambiguously aligned regions within the ITS1 spacer is the hypervariable region ITS1-HR sensu Miadlikowska & al. (2003), which varies greatly in length and can contain microsatellites with single nucleotide strings or short repeats. We re-delimited the ITS1-HR locus (sites 111–237 of the ITS1 alignment from Miadlikowska & al., 2003) to include additional variable sites (a total fragment corresponding to positions 182–335 of the ITS1 alignment). The inclusion of conserved flanking sites helped to extend the use of the ITS-HR as a powerful taxonomic marker, at the species level, to the entire section *Peltigera*. We added an ITS sequence from *P. spuriella* and 175 sequences from GenBank to our dataset (Electr. Suppl.: Table S6). No ITS1 sequence was available for *P. fimbriata*. A total of 201 different sequences of the ITS1-HR region were present among the 537 individuals from section *Peltigera* for which ITS sequences without missing/ambiguous data were available. Eighty-three of these sequences were found in more than one individual whereas the remaining 118 were unique (Electr. Suppl.: Fig. S2). The sequences varied in length from sixteen sites (conserved flanking region only) in *P. islandica* and its sister species *P.* sp. 20, to 137 nucleotides in *P. membranacea* 1 (Electr. Suppl.: Fig. S2). With some rare exceptions where identical sequences were shared among different putative species (e.g., *P. islandica* with *P.* sp. 20; *P. antarctica* with *P. ponojensis*/*monticola* 1 and 2; *P. granulosa* with *P. papuana* and *P. friesiorum*), overall, sequences of the ITS1-HR were more similar within than among species.

■ DISCUSSION

Species delimitation in *Peltigera* sect. *Peltigera* and sect. *Retifoveatae*. — Overall the phylogeny for section *Peltigera* (Fig. 1) is in agreement with the topology recovered by Miadlikowska & al. (2003), which was based on ribosomal loci together with the recoded ambiguous regions (including ITS1-HR) and a considerably smaller set of species mostly from Europe and North America. Our phylogeny (Fig. 1) is more robust, as many previously unresolved or poorly supported relationships among and within major clades received high support. A single discrepancy between these two studies involved the placement of the *P. cinnamomea* clade (clade 7), which is sister to clade 4–6 (Fig. 1) versus clade 8–9 in Miadlikowska & al. (2003).

The proportion of uncovered biodiversity in section *Peltigera* is remarkably high (57%) (Fig. 2), but perhaps not unexpected considering earlier studies that had highlighted a phylogenetic structure indicative of several species complexes (e.g., Goffinet & al., 2003; Miadlikowska & al., 2003). Furthermore, the dramatic increase in species richness in this section parallels the trend emerging from inferences based on DNA data in other lineages of Peltigerales (Moncada & al., 2014a, b; Lücking & al., 2017; Magain & al., 2017a, b; Simon & al., 2018), as well as in other groups of lichen-forming fungi. Similar to our findings, many widespread morphospecies were split into numerous more restricted phylogenetic species in the genera *Rhizoplaca* Zopf (Lecanoraceae, Leavitt & al., 2011), *Melanohalea* O.Blanco & al. (Parmeliaceae, Leavitt & al., 2013) and *Protoparmelia* M.Choisy (Parmeliaceae, Singh & al., 2015). Extreme examples include the presence of hundreds of undiscovered species in overlooked groups, especially in tropical regions, such as in the genus *Cora* Fr. (although based on a single marker [ITS]) or the family Graphidaceae (Lücking & al., 2014a, b). The high discrepancies between the phylogeny-based species delimitation methods on one hand, and traditional morphospecies on the other hand, leads to questioning the adequacy of using morphology as the leading criterion for describing lichen-forming fungal species (Lumbsch & Leavitt, 2011).

A recent study by Sukumaran & Knowles (2017) demonstrated that species delimitation methods relying on multispecies coalescence can interpret lineages reflecting intraspecific genetic structure as different species and, therefore, can inflate species biodiversity. Cases involving known morphology-based species that were validated phylogenetically as monophyletic, but that are split into multiple species by species delimitation methods, can represent structured intraspecific populations. Consequently, the resulting nested sister species are often phenotypically cryptic. Combining several methods can improve species delimitation (Carstens & al., 2013) but results can only be as good as the amount and quality of the data available, and the performance of the methods used.

Three main geographic patterns underlined the resulting species delimitations in section *Peltigera* (Fig. 5): (1) monophyletic morphospecies divided into several sympatric species (e.g., *P. austroamericana*/*P. fibrilloides* [six lineages] and *P. lacinia-ta* [two lineages in the Neotropics], *P. montis-wilhelmii* and *P. erioderma* [two lineages for each, in Papua New Guinea], and *P. lepidophora* [two lineages in the Northern Hemisphere]); (2) monophyletic morphospecies divided into several species showing distinct geographic patterns (e.g., *P.* "*neocanina*" [four lineages, of which two occur in North America, one in Asia and one in Europe], *P.* "*neorufescens*" 1–5 [five lineages, two of which are in North America, one in Europe and two in the Neotropics]); (3) monophyletic morphospecies divided into several species showing restricted geographic pattern (e.g., *P. degenii* [three main groups, one in Europe, the second one mostly in North America, but also present in Asia, and the third group is found in Asia; the latter lineage was additionally divided into three lineages, well corroborated with geographic patterns, i.e., Sakhalin vs. Honshu vs. Kurile Islands and Jilin], *P. ponojensis*/*monticola* complex [fourteen species with partially overlapping distributions, together with the Neantarctic *P. antarctica* and the Neotropical *P.* sp. 17 being part of this clade (Fig. 5). *Peltigera canina* is another well-known species divided into two species – one mostly restricted to North America and the other with almost a cosmopolitan distribution, while both putative species co-occur in Iceland and North America.

In our study, some putative species, such as *P. canina* 1 and 2 were represented by a large number of individuals (20 or more specimens), whereas others, such as within morphospecies *P. lepidophora*, *P.* "*neorufescens*" and *P.* "*neocanina*",

include a single or often no more than two specimens (Fig. 2; Electr. Suppl.: Fig. S2). Singleton species are very common in species delimitation studies, and it has been suggested that in most cases they result from undersampling (Coddington & al., 2009). However, simulation studies showed that the GMYC model still performs well in the presence of large amounts of singleton species (Fujiawa & Barraclough, 2013). Whether *Peltigera* singletons represent distinct species or artifacts of the implemented methods awaits further testing based on additional samples bridging the current localities (often distant) and using complementary methods that rely on other models with different assumptions.

Our analyses confirmed that some taxa introduced informally in previous studies (Miadlikowska & Lutzoni, 2000; Miadlikowska & al., 2003; Jüriado & al., 2017) represent undescribed species, or assemblages of undescribed species, delimited consistently by multiple methods (e.g., *Peltigera* "*fuscopraetextata*", *P.* "*neocanina*" and *P.* "*neorufescens*"). Other provisionally named taxa should be merged (as indicated by Miadlikowska & al., 2003), such as *P.* "*pallidorufescens*", which is synonymous with *P.* "*fuscopraetextata*", and *P.* "*fuscoponojensis*" which is nested within the *P.* "*neorufescens*" clade. The specimen of *P.* "*scotteri*" 1 included in Miadlikowska & al. (2003) belongs to *P. ponojensis*/*monticola* 10, whereas *P.* "*scotteri*" 2 represents *P. degenii* 2a. The collection of *P.* "*latopraetextata*" 1 falls within *P. cinnamomea*, *P.* "*latopraetextata*" 3 belongs to *P. praetextata*, *P.* "*boreorufescens*" 1 represents *P. canina* 2, and *P.* "*boreorufescens*" 2 belongs to *P.* "*neocanina*" 1. These provisional names will be corrected in all relevant GenBank records.

A recent study (Jüriado & al., 2017) reported a high level of undescribed species in section *Peltigera* collected in Estonia. Several lineages recognized by the authors based on ITS sequences correspond to species delimited in this study using multiple loci and methods. For example, Estonian lineages of *P. didactyla* I, II, and III represent *P. didactyla* 1 (*P.* sp. 2 in Goffinet & al., 2003), *P. didactyla* 3 (*P. didactyla* s.str. in Goffinet & al., 2003), and *P. didactyla* 2 (*P.* sp. 3 in Goffinet & al., 2003), respectively. *Peltigera lepidophora* from Jüriado & al. (2017) corresponds to our *P. lepidophora* 1, a species already known from Europe and North America and their *P.* aff. *neocanina* corresponds to our *P.* "*neocanina*" 4, collected in Norway and Iceland. Apart from the hyperdiverse *P.* "*neorufescens*" complex, all lineages detected in section *Peltigera* by Jüriado & al. (2017) were also sampled in our study. Furthermore, several species that were thought to occur exclusively or predominantly in North America seem to have much broader ranges as suggested by the recent records for *P. canina* 2 (corresponding to *P. canina* I), *P.* "*neorufescens*" 5 (corresponding to *P. neorufescens*), and *P.* "*neocanina*" 1 (corresponding to *P. neocanina*) from Estonia (Jüriado & al., 2017).

We reassessed the utility of the ITS1 hypervariable region (ITS1-HR) as a reliable tool to distinguish species in section *Peltigera* and *Retifoveatae* proposed by Miadlikowska & al. (2003). As in 2003, we found that sequences of the ITS1-HR were more similar within the majority of the monophyletic lineages delimited as species than among them, and therefore, this hypervariable region continues to be a powerful marker to identify most species. However, we also have rare cases where morphologically distinct sister species have sometimes identical ITS1-HR sequences (e.g., *P. friesiorum*/*P. papuana*/*P. granulosa*; Electr. Suppl.: Fig. S2). Occurrences of similar types of ITS1-HR sequences across multiple recognized species, were overall rare and mostly restricted to large species complexes such as *P. ponojensis*/*monticola*, where phylogenetic relationships among putative species are not well established and poorly supported (Fig. 1; Electr. Suppl.: Fig. S2). In this clade, the morphotypes corresponding to *P. ponojensis* and *P. monticola* were rarely segregated into separate species and mostly mixed together across multiple delimited species. One of the few exceptions are the morphologically unique *P.* sp. 17 (the only species in this clade with sorediated isidia) that resembles *P. boulydelesdainii* Gyeln. (except for the absence of secondary metabolites), however its ITS-HR region is similar or identical to sequences recorded in other members of the *P. ponojensis*/*monticola* clade (Electr. Suppl.: Fig. S2). The description of *P. plittii* Gyeln. (type specimen collected in Colorado, U.S.A.) matches morphotypes of *P. ponojensis*/*monticola* 8, however, the disentanglement of this entire species complex requires a separate comprehensive revision.

Our results also suggest that *P. fibrilloides* and *P. austroamericana* (morphologically distinct; i.e., the tomentous versus glabrous upper thallus of *P. fibrilloides* versus *P. austroamericana* morphotypes, among other differences) may represent the same species because individuals growing intermixed in nature were mixed phylogenetically, and share the same ITS1-HR sequence (Fig. 1; Electr. Suppl.: Fig. S2). Another case of two named species with identical ITS1-HR sequences, includes *P. koponenii*, from Papua New Guinea, which is nested within *P. canina* 1 (representing *P. canina* s.str.), which together are separated from *P. canina* 2, a new putative species known from North America, Iceland and Estonia (Figs. 1 and 2; Electr. Suppl.: Fig. S2). Although our analyses recognized two putative species, the high similarity in the ITS1-HR region suggests that *P.* sp. 20, known only from British Colombia, should be merged with *P. islandica* as already indicated by Manoharan-Basil & al. (2016). A broader distribution of *P. islandica* is also in agreement with the recent report of *P. islandica* in Estonia (Jüriado & al., 2017). We used the name *P. antarctica* (described by Dodge, 1968, from Antarctica) for a clade in *P. ponojensis*/*monticola* complex encompassing a set of specimens morphologically and geographically consistent with *P. patagonica*, however, phylogenetically unrelated and associated with different cyanobionts (phylogroup XXVIII in *P. patagonica*, but VI, XXX, and XXV in *P. antarctica*). *Peltigera austroamericana*/*fibrilloides* 5 encompasses typically glabrous species and could correspond to *P. austroamericana* s.str. The name *P. ecuadoriana* Gyeln. is available for one of the recognized lineages of this clade. Finally, *P. spuriella* potentially represented by two specimens (P1648, P1731) seems to be closely related to *P. friesiorum*, based on the phylogeny and similarity of their ITS-HR region. Despite their distinct thallus morphology, both species were often considered conspecific by most species delimitation methods.

Heterogeneity of nucleotide substitution rates: sorediate, fast growing, species have higher rates of evolution. — We estimated that the nucleotide substitution rates are nearly two times faster in clade 4 (*P. didactyla* clade) compared to clades 5–7 in section *Peltigera* (Fig. 1). All species in clade 4 produce asexual propagules (soredia) and therefore, can disperse both the fungal and cyanobacterial partners simultaneously (i.e., vertical transmission of the cyanobiont). Two other sorediate species, *P.* sp. 17 and *P. granulosa*, which are placed outside of clade 4, i.e., among non-sorediate taxa in clades 5 and 6, respectively, do not seem to evolve at a faster rate. Overall, our results seem to contradict the expectation of higher evolutionary rates in sexually reproducing species compared to asexually reproducing species (see Melián & al., 2012, for a discussion; Rydholm & al., 2006). However, most of the species in clade 4 also reproduce sexually as suggested by the common presence of apothecia on their thalli. Compared to the majority of species from other clades (Vitikainen, 1994), species in clade 4 (e.g., *P. didactyla* and *P. ulcerata*) are typical early successional lichens with very small and fast growing thalli, often with apothecia (*P. didactyla*), and consequently probably have a drastically shorter generation time, leading to higher evolutionary rates, as it was suggested for animals (Martin & Palumbi, 1993). The fact that they also show very broad geographic distributions (Fig. 5) may also contribute to larger population sizes. Another result supporting higher evolutionary rates and/or population sizes for clade 4 is that the estimated value of θ for bPP analyses, which was higher than for all other clades (0.02 vs. 0.0025–0.0044) in section *Peltigera*. Other factors have been proposed for explaining variation in substitution rates in lichen-forming fungi, such as changes in ecological conditions. It was suggested that evolutionary rates were higher in parmelioid lichens growing in tropical and oceanic habitats compared to those in more arid habitats (Lumbsch & al., 2008). Otálora & al. (2013a) reported that clades including species from tropical and humid habitats have higher evolutionary rates in the Collemataceae. We have not detected this trend in section *Peltigera*.

Biogeographical patterns in *Peltigera* sect. *Peltigera*. — Four of the five early diverging species, i.e., *Peltigera* sp. 14 and *P. aubertii*, *P. frigida* and *P. patagonica* (Fig. 5) are restricted to southern Chile and Argentina. The most recent common ancestor of section *Peltigera* could have inhabited the Neantarctic region of South America. A similar result was found in the genus *Flavoparmelia* Hale (Parmeliaceae), which comprises several subcosmopolitan species and whose origin was reconstructed in South America (Del-Prado & al., 2013). Most ancestors at the deepest nodes of the phylogeny seem to have originated in Asia and North America (Fig. 5). One possible scenario leading to the current distribution of species would have been a dispersion north from the Neantarctic to the Pacific Northwest, followed by a dispersion across North America and to Asia. An alternative scenario could involve a more broadly distributed ancestor than the extant species and, consequently, the current Neantarctic species would be the result of paleoendemism. The ancestor of clade 4 (sorediated, fast growing, species) was inferred to occur in the Neotropics, clades 5 and 6 (and potentially clades 4–6) in North America, and clade 8–9 in Asia. Most species in clade 9 may have diversified in the Pacific Northwest region, before the *P. austroamericana*/sp. 22 group dispersed to the Neotropics (Fig. 5).

The biogeographical analyses highlight at least five dispersion events to the Neotropics, all most likely from a Beringian origin (i.e., the ancestors of clade 4, the *P. laciniata*/sp. 15 group, the *P.* "*neorufescens*" 1 and 2 clade, *P.* sp. 17 and the *P. austroamericana*/sp. 22 group; Fig. 5). A similar pattern was detected in section *Polydactylon* for *Peltigera* sp. 6, which is sister to the panboreal *P. occidentalis* (Å.E.Dahl) Kristinsson (Magain & al., 2017a). With the exception of clade 4, all these southern dispersion events were relatively recent in the history of the section. The reverse scenario seems to be plausible within clade 4 where the ancestral taxa were likely to be Neotropical, and very widespread species such as *P. extenuata* and *P. didactyla*, or their ancestors dispersed from this area to reach their current subcosmopolitan ranges. Only two inferred dispersion events (with the exception of subcosmopolitan species), for *P. antarctica* and *P.* "*fuscopraetextata*" were to the Neantarctics and occurred rather from North America than from the Neotropics. This pattern differs from the observation in section *Polydactylon*, where the only Neantarctic species, *P. truculenta*, originated from a Neotropical group (Magain & al., 2017a).

Dispersion to Australasia could have occurred from Asia (for *P. tereziana*) but also from the Americas, i.e., the Neotropics for the ancestor of the clade comprising *P. papuana* and *P. granulosa*, and from North America for the ancestor of *P. fimbriata* (Fig. 5). Except for the sorediate species from clade 4 (*P. ulcerata*, *P. didactyla*), the remaining subcosmopolitan species, such as *P. canina* 1 or *P. praetextata*, are absent from the Neotropics. In two cases (*P. extenuata* 1 and 2, *P. rufescens* 1 and 2), the neotropical members of the morphospecies appear as a sister species to a clade containing widespread and morphologically similar individuals from other regions, including Neantarctic (bipolar distribution). This pattern may suggest that climatic differences were a barrier impacting species distribution more than geographic distance. The importance of climate in shaping the ranges of both mycobionts and photobionts, has been shown in *Peltigera* (Magain & al., 2017a; Lu & al., 2018), other genera of lichenized fungi, such as *Cetraria* Ach. (Fernández-Mendoza & al., 2011) and *Protoparmelia* (Singh & al., 2016), as well as in bryophytes (Lewis & al., 2014).

Contrary to clade 4, which encompasses widespread sorediate, fast growing, species, most broadly distributed species are sister to species with very limited ranges. Examples include *P. rufescens* 1, part of a group of eleven species, each restricted to a single region, *P. canina* 1, closely related to *P. islandica* and *Peltigera* sp. 20, restricted to Iceland and to the Pacific Northwest, respectively, and *P. praetextata*, sister to *P. evansiana*, known only from North America.

A recent study questioned the use of DEC and DEC+J models because they inflate the contribution of cladogenetic events to the likelihood (Ree & Sanmartín, 2018). Our study did not aim to detect the relative impacts of cladogenesis and

anagenesis, but rather to reconstruct the global biogeographic patterns in section *Peltigera*. Overall, four of the six models tested (DEC, DEC+J, DIVALIKE, DIVALIKE+J) globally agree on the reconstruction of the geographical distribution of the ancestors of the main clades discussed in the results section (Neotropical for clade 4, North American for clades 5 and 6, Asian for clades 8, 9 and the common ancestor of clades 4–9). Results with one model, BAYAREALIKE, suggest that the ancestors at the deep nodes had worldwide distributions, and that current species distributions are the result of drastic reductions of their ranges. Results with BAYAREALIKE+J are somewhat intermediary, suggesting a Holarctic distribution for most of these deep nodes.

Evolution and ecology of symbiotic specificity. — In general, it seems that the specificity of *Peltigera* species towards their cyanobionts is driven in part by the mode of reproduction, at least in clade 4, where many sorediate species associate with fewer cyanobionts than members of other clades (Fig. 5). Exceptions include *P. didactyla* s.l., which seems to behave like a generalist, but this species, unlike *P. ulcerata* s.l. and *P. extenuata* s.l., frequently produce apothecia (Vitikainen, 1994; Miadlikowska & Lutzoni, 2000; Goffinet & al., 2003) and hence the horizontal transmission of the photobiont in *P. didactyla* may account for the lower specificity observed. Outside of clade 4, the occurrence of asexual propagules, allowing the vertical transmission of the photobiont, also leads to higher specificity compared to species lacking vegetative propagules. Sorediate (*P.* sp. 17), isidiate (*P. evansiana*) or phyllidiate (*P.* "*fuscopraetextata*") species consistently have higher levels of specificity. Similarly, among two species in the genus *Pectenia* P.M.Jørg. & al. (former *Degelia* Arv. & D.J.Galloway), a vegetatively reproducing species was reported to be more specialized than its sexually reproducing close relative (Otálora & al., 2013b). Otálora & al. (2010) also found high levels of specificity in several species reproducing through asexual propagules in the family Collemataceae compared to closely related but sexually reproducing species. However, other studies (Wornik & Grube, 2010; Leavitt & al., 2015) on lichens involving green algae, instead of *Nostoc*, did not report a direct link between the reproduction mode and specificity.

Among the species for which we sequenced cyanobionts from more than five thalli, we found one strict mycobiont specialist – *P. tereziana*, that was associated with only one *Nostoc* phylogroup (Fig. 4B). Cases of strict specialists with lower *Nostoc* sampling include *Peltigera vainioi*, *P. retifoveata*, *P. patagonica*, *P. papuana* and *Peltigera* sp. 14. The fact that these species were found with a relatively rare *Nostoc* phylogroups (XXXVIa, XXXVIIIa, XXXI, and XXIII, respectively) may suggest that the observed specificity is real, whereas high specificity in *P. degenii* 3b and *Peltigera* sp. 19, which were only collected three times each, and always with very widespread phylogroups (V and VI, respectively) may be an artifact of a low sampling. Species sampled many times with a common phylogroup (such as *P.* "*fuscopraetextata*" with phylogroup VI) probably represent real cases of specialization on a widespread and generalist *Nostoc* phylogroup (Fig. 5; Electr. Suppl.: Table S1).

Many of the specialist species in section *Peltigera* have narrow geographic ranges and often have specific ecological niches, such as *Peltigera* sp. 14, which was collected in Chile from relatively wet to semi-aquatic habitats. *Peltigera patagonica* and *P. aubertii* were only found in the Neantarctic region, and *P. vainioi* is a rare species in the Neotropics. The distribution of *P. retifoveata* is restricted to the boreal zone, whereas *P. tereziana* occurs in Australia and New Zealand, and *P. papuana* in Papua New Guinea. A similar trend was reported for species from section *Polydactylon* (Magain & al., 2017a) and outside of the genus *Peltigera*, in *Pectenia* (Otálora & al., 2013), and in the family Collemataceae (Otálora & al., 2010), where specialist species have smaller ranges and are more restricted ecologically. At the other end of the spectrum, cosmopolitan or subcosmopolitan species, such as *P. canina* 1 (= *P. canina* s.str.), *P. rufescens* 1, *P. ponojensis*/*monticola* 9 or *P. praetextata* are generalists. At a global spatial scale (see Chagnon & al., 2018), this inverse correspondence between the level of specificity and geographic range of the mycobiont suggests that the ability to associate with a wider spectrum of photobionts increases the potential of a species to occupy greater geographical areas, whereas specialists restricted to one cyanobacterial partner might be limited by the availability of their cyanobiont, especially if the *Nostoc* phylogroup has a narrow distribution and is not a generalist. Another strategy leading to a larger range is to be specialized on a widespread and generalist phylogroup, such as *P.* "*fuscopraetextata*" with phylogroup VI or *P. membranacea* 1 with phylogroup XVI. A similar pattern was detected in section *Polydactylon* (Magain & al., 2017a) for *P. polydactylon* being a specialist with the common and generalist phylogroup V and *P. hymenina* often found with widespread and generalist phylogroup XVI.

True generalist interactions should involve frequent associations between the most abundant partners, as well as several rare interactions with rare partners (Vázquez & al., 2007). Such a pattern was observed in several cases in section *Peltigera*. For example, in South America, *P. friesiorum* was found multiple times associated with the widespread phylogroups V (eight times) and XXXIX (five times) in addition to four unique interactions. This is also the case for *P. canina* 1, *P. praetextata*, *P.* "*neocanina*" 1, and *P. austroamericana* 5, which associate frequently with phylogroup V but were also reported several times with other, less common phylogroups. Photobionts can show a similar pattern, for example *Nostoc* phylogroup V is frequently found (seven to eight times) with common species such as *P. canina* 1, *P. friesiorum* and *P. praetextata*, but in addition was sometimes reported with rare species such as *P. granulosa*, *P. montis-wilhelmii* 1 or *P. wulingensis* (Fig. 3; Electr. Suppl.: Table S1). Our results confirm specificity patterns observed in section *Peltigera* at a local scale (O'Brien & al., 2013). In general, *Peltigera* species that are generalists at an intercontinental scale might appear to be more specialized at a local scale, such as *P. canina* 1 and 2, which are mostly specialized on *Nostoc* from phylogroup VI in British Columbia (O'Brien & al., 2013) but are generalists at a global scale. Chagnon & al. (2018) also showed a higher asymmetry at local scales (several specialist mycobionts associating with

one or two generalist *Nostoc* phylogroups), compared to more symmetric associations at a global scale.

Within section *Peltigera*, clade 4 differs from other clades in several aspects. It includes morphologically distinct species with generally small, fast growing, thalli and with asexual propagules (soralia). This clade has the highest number of widespread species, with five of ten species occurring in three or more biogeographic regions while other clades contain no (clade 5, clade 7) or only a few species (one in clade 6, two in clade 8 and three in clade 9) with such broad distributions. Clade 4 has the highest average Specificity index (0.64 vs. 0.41–0.57 for other clades), the greatest number of species (three) associated with a single *Nostoc* phylogroup, as well as significantly higher rates of nucleotide substitutions (Table 1).

In summary, most species in section *Peltigera* show a relatively low level of specificity compared to section *Polydactylon* (Magain & al., 2017a). This could be due to differences in ecological requirements, as members of the *canina* group seem to be more ubiquitous compared to species from section *Polydactylon*, which are found mostly in boreal areas and at high elevations. This difference could also be due to the recent origin of many of the species in section *Peltigera*, which is the most speciose section of the genus *Peltigera*. Most specialists in section *Peltigera* either originated early during the evolution of the section (clades 2a–c; Figs. 1 and 5) or reproduce through vegetative propagules (clade 4; Figs. 1 and 5). Unlike section *Polydactylon*, section *Peltigera* includes several very widespread, almost cosmopolitan species. Large distributions should favor the maintenance of a generalist selection of photobionts, allowing these species to grow in a higher number of ecological and geographical environments. Future challenges include the formal description of putative species revealed by this study, following further validations using multidisciplinary approaches based on population genetics, phylogenomics, network analyses and physio-ecological studies. A global phylogenetic study of the genus *Peltigera* is now needed to enhance our understanding of its biodiversity, biogeography and patterns of symbiotic interactions.

■ AUTHOR CONTRIBUTIONS

NM designed this study, generated data, ran analyses and wrote the paper. CT designed this study, generated data, ran analyses and contributed to the writing of this article. DN generated data and edited the manuscript. TG, BG, ES and OV contributed to the taxonomy and systematics of this study, and edited the manuscript. JM and FL designed the entire project, including this study, they oversaw the implementation of every phase and aspects of this study, mentored two postdoctoral researchers (CT and NM), and co-wrote the manuscript with NM. — ORCID: NM, https://orcid.org/0000-0001-5409-9518; BG, https://orcid.org/0000-0002-2754-3895; ES, https://orcid.org/0000-0002-0456-0131

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Appendix 1. Taxon sampling for *Peltigera* sect. *Peltigera* and sect. *Retifoveatae* and five outgroup species, with associated voucher information, including mycobiont and cyanobiont sequences. Newly generated sequences are indicated in bold. An extended version is available in the Electronic Supplement as Table S1 and includes clade numbers, DNA id and (when applicable) the cyanobiont *rbcLX* phylogroup.

Peltigera aphthosa (L.) Willd., U.S.A.: AK, *Miadlikowska s.n.* (OSC), –, **MH771012, MH770256, MH770507, MH770009,** –; ***P. antarctica*** C.W.Dodge, Chile: Region XII, *Goffinet 6837* (CONN) , **MH758271, MH770824, MH770051, MH770300, MH769795,** KX923110; ***P. antarctica*** C.W.Dodge, Chile: Region XI, *Rubio 4073* (H), **MH758272, MH770825, MH770052, MH770301, MH769796, MH770563; *P. antarctica*** C.W.Dodge, South Orkney Islands, *Lindsay 935* (H), **MH758275, MH770826,** –, –, –, –; ***P. antarctica*** C.W.Dodge, Argentina, *Stenroos 1954* (H), **MH758270,** –, **MH770053, MH770302,** –, **MH770564; *P. antarctica*** C.W.Dodge, Chile: Region XII, *Goffinet 10521-2* (CONN), **MH758273, MH770827, MH770054, MH770303, MH769797, MH770565; *P. antarctica*** C.W.Dodge, Chile: Region X, *Wheeler & Nelson 5893* (CONC), **MH758274, MH770828, MH770055, MH770304, MH769798, MH770566; *P. aubertii*** C.W.Dodge, Chile: Region XII, *Stenroos 2459* (H), **MH758229, MH770812,** –, –, –, –; ***P. aubertii*** C.W.Dodge, Chile: Region XII, *Goffinet 10559* (CONN), **MH758230, MH770813, MH770013, MH770259, MH769760, MH770512; *P. aubertii*** C.W.Dodge, Chile: Region XII, *Shaw 18004* (DUKE), **MH758231,** –, –, –, –, **MH770513; *P. aubertii*** C.W.Dodge, Chile: Region XII, *Goffinet 10558* (CONN), **MH758232,** –, –, –, –, **MH770514; *P. aubertii*** C.W.Dodge, Chile: Region X, *Wheeler & Nelson 3191* (CONC), **MH758233, MH770814, MH770014, MH770260, MH769761, MH770515; *P. aubertii*** C.W.Dodge, Chile: Region X, *Wheeler & Nelson 5870* (CONC), **MH758234,** –, **MH770015, MH770261,** –, **MH770516; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **1,** Costa Rica, *Miadlikowska & Lutzoni 23.03.03-10* (DUKE 0357975), **MH758454, MH770954,** –, –, –, **MH770742; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **1,** Colombia, *Dumont & al. 4066* (H), **MH758440, MH770955, MH770185, MH770444,** –, **MH770743; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **2,** Mexico, *Herrera-Campos 13380* (MEXU), **MH758442, MH770956, MH770186, MH770445, MH769940, MH770744; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **2,** Mexico, *Herrera-Campos 13381* (MEXU), **MH758462, MH770957, MH770187, MH770446, MH769941, MH770745; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **3,** Peru, *Lutzoni 05.23.212-7* (DUKE 0357974), **MH758465, MH770958, MH770188, MH770447, MH769942, MH770746; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **3,** Peru, *Rivas Plata & Ramos s.n.* (DUKE 0357973), **MH758466, MH770959, MH770189, MH770448, MH769943, MH770747; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **3,** Colombia, *Lücking 33628* (UDBC), **MH758451, MH770960, MH770190, MH770449, MH769944, MH770748; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **3,** Ecuador, *Truong 3975* (DUKE 040152), **MH758460, MH770961, MH770191, MH770450, MH769945, MH770749; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **4,** Costa Rica, *Miadlikowska & Lutzoni 23.03.03-8* (DUKE 0401856), **MH758453, MH770962, MH770192, MH770451, MH769946, MH770750; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **4,** Costa Rica, *Miadlikowska & Lutzoni 23.03.03-15* (DUKE 0401855), **MH758455, MH770963,** –, –, –, **MH770742; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **4,** Costa Rica, *Miadlikowska & Lutzoni 23.03.03-21* (DUKE 0401857), **MH758456, MH770964,** –, –, –, **MH770743; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **4,** Costa Rica, *Miadlikowska & Lutzoni 22.03.03-37* (DUKE 0401853), **MH758457, MH770965,** –, –, –, **MH770744; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **4,** Mexico, *Herrera-Campos 137* (MEXU), **MH758461, MH770966, MH770193, MH770452, MH769947, MH770745; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **4,** Costa Rica, *Miadlikowska & Lutzoni 22.03.03-21* (DUKE 0401854), **MH758458,** –, –, –, –, –; ***P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **5,** Brazil, *Miadlikowska & al. s.n.* (CGMS 34505), **MH758438, MH770967, MH770194, MH770453, MH769948, MH770751; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **5,** Peru, *Miadlikowska s.n.* (DUKE), **MH758443,** –, –, –, –, **MH770752; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **5,** Brazil, *Canez 10234* (CGMS 35044), **MH758447, MH770968, MH770195, MH770454, MH769949, MH770753; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **5,** Brazil, *Magain s.n.* (CGMS 34427), **MH758448, MH770969, MH770196, MH770455, MH769950, MH770754; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **5,** Ecuador, *Kalb 18391* (DUKE), **MH758459, MH770970, MH770197,** –, **MH769951, MH770755; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **5,** Brazil, *Miadlikowska s.n.* (CGMS 34409), **MH758449,** –, –, –, –, **MH770756; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **5,** Bolivia, *Kukwa 8504* (ex UGDA-L-17700, DUKE dupl. 0401859), **MH758445, MH770971, MH770198, MH770456, MH769952, MH770757; *P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **5,** Bolivia, *Truong 2826* (DUKE 0401858), **MH758446, MH770972, MH770199, MH770457, MH769953,** –; ***P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **5,** Peru, *Lutzoni 05.23.2012-13* (DUKE 0357966), **MH758464,** –, –, –, –, –; ***P. austroamericana*** Zahlbr./***fibrilloides*** (Gyeln.) Vitik. **6,** Peru, *Bennett s.n.* (WIS), **MH758444, MH770973, MH770200, MH770458, MH769954, MH770758; *P. austroamericana*** Zahlbr. s.l., Colombia, *Lücking 33653* (UDBC), **MH758450,** –, –, –, –, **MH770733; *P. austroamericana*** Zahlbr. s.l., Mexico, *Barcenas-Penas 1233* (MEXU), **MH758441,** –, –, –, –, **MH770734; *P. austroamericana*** Zahlbr. s.l., Peru, *Miadlikowska s.n.* (DUKE 0357967), **MH758463,** –, –, –, –, **MH770735; *P. austroamericana*** Zahlbr. s.l., Brazil, *Miadlikowska & al. s.n.* (CGMS 34490), **MH758439,** –, –, –, –, **MH770736; *P. austroamericana*** Zahlbr. s.l., Peru, *Rivas Plata & Ramos s.n.* (DUKE 0357971), –, –, –, –, –, **MH770737; *P. austroamericana*** Zahlbr. s.l., Colombia, *Lücking 33631* (UDBC), **MH758452,** –, –, –, –, **MH770738; *P. canina*** (L.) Willd. **1,** Canada: BC, *O'Brien 020708-4-5-1* (DUKE), FJ708890, –, **MH770201, MH770459, MH769955,** KC437709; ***P. canina*** (L.) Willd. **1,** Canada: BC, *O'Brien 030611-0-0-6* (DUKE), FJ708881, FJ709294, **MH770202, MH770460, MH769956,** –; ***P. canina*** (L.) Willd. **1,** Iceland, *Miadlikowska & Lutzoni s.n.* (DUKE 0357980), KU954063, KM005803, **MH770203, MH770461, MH769957,** KX923097; ***P. canina*** (L.) Willd. **1,** Russia: Krasnoyarsk Territory, *Miadlikowska & Lutzoni s.n.* (DUKE 0357997), **MH758475, MH770974,** –, –, **MH769958, MH770759; *P. canina*** (L.) Willd. **1,** Russia: Krasnoyarsk Territory, *Miadlikowska & Lutzoni s.n.* (DUKE 0401822), **MH758475,** –, –, –, –, **MH770760; *P. canina*** (L.) Willd. **1,** Papua New Guinea, *Sérusiaux s.n.* (LG), –, –, –, –, –, **MH770761; *P. canina*** (L.) Willd. **1,** Russia: Krasnoyarsk Territory, *Miadlikowska & Lutzoni s.n.* (DUKE 0401836), **MH758478, MH770975, MH770204, MH770462, MH769959, MH770762; *P. canina*** (L.) Willd. **1,** China: Yunnan, *Miadlikowska s.n.* (DUKE 0401862), **MH758470, MH770976, MH770205,** –, **MH769960, MH770763; *P. canina*** (L.) Willd. **1,** Austria, *Hafellner & Miadlikowska s.n.* (DUKE 0130114), **MH758467, MH770977, MH770206, MH770463, MH769961, MH770764; *P. canina*** (L.) Willd. **1,** France: Corsica, *Vust 6421* (G), **MH758471, MH770978, MH770207, MH770464, MH769962, MH770765; *P. canina*** (L.) Willd. **1,** Switzerland, *Vust 279* (G), **MH758479, MH770979, MH770208, MH770465, MH769963, MH770766; *P. canina*** (L.) Willd. **1,** France: Corsica, *Vust 6412* (G), **MH758473, MH770980, MH770209, MH770466, MH769964, MH770767; *P. canina*** (L.) Willd. **1,** Papua New Guinea, *Aptroot 32283* (H), –, –, –, –, –, **MH770768; *P. canina*** (L.) Willd. **1,** Papua New Guinea, *Sérusiaux s.n.* (LG), **MH758472, MH770981, MH770210,** –, –, –; ***P. canina*** (L.) Willd. **1,** The Netherlands, *Aptroot 53752* (ABL), **MH758474, MH770982, MH770211, MH770467, MH769965, MH770769; *P. canina*** (L.) Willd. **1,** Canada: BC, *Goward 5305* (UBC), **MH758469, MH770983, MH770212, MH770468, MH769966, MH770770; *P. canina*** (L.) Willd. **2,** Canada: BC, *O'Brien 020708-31-5-2* (DUKE), FJ708874, FJ709304, **MH770213,** –, **MH769967,** –; ***P. canina*** (L.) Willd. **2,** Canada: BC, *O'Brien 020708-70-5-2* (DUKE), FJ708876, FJ709303, –, –, –, –; ***P. canina*** (L.) Willd. **2,** Canada: BC, *O'Brien 020708-70-1-3* (DUKE), FJ708875, FJ709304, **MH770216, MH770469, MH769968,** –; ***P. canina*** (L.) Willd. **2,** Iceland, *Miadlikowska & Lutzoni 08.08.10-3* (DUKE 0401829), KU954062, KM005821, **MH770217, MH770470, MH769969,** KX923096; ***P. canina*** (L.) Willd. **2,** U.S.A.: NC, *Miadlikowska & Lutzoni s.n.* (DUKE 0357998), **MH758480,** –, **MH770218,** –, –, **MH770771; *P. canina*** (L.) Willd. **2,** U.S.A.: NC, *Miadlikowska & Lutzoni s.n.* (DUKE 0401827), –, –, **MH770219,** –, –, **MH770772; *P. canina*** (L.) Willd. **2,** U.S.A.: NC, *Miadlikowska & Lutzoni s.n.* (DUKE 0358000), **MH758481,** –, **MH770220,** –, –, **MH770773; *P. canina*** (L.) Willd. **2,** U.S.A.: NC, *Lutzoni & Miadlikowska s.n.* (DUKE 0401828), **MH758475,** –, **MH770221,** –, –, KX923113; ***P. canina*** (L.) Willd. **2,** U.S.A.: MO, *Buck 48584* (NY 00729928), **MH758482,** –, **MH770222,** –, –, **MH770774; *P. canina*** (L.) Willd. **2,** U.S.A.: NC, *Miadlikowska & Lutzoni s.n.* (DUKE 0357999), **MH758483, MH770984, MH770223, MH770471, MH769970, MH770775; *P. canina*** (L.) Willd. **2,** U.S.A.: NC, *Hollinger 2731* (UBC), **MH758484, MH770985, MH770224, MH770472, MH769971, MH770776; *P. canina*** (L.) Willd. **2,** U.S.A.: OK, *Buck 46463* (DUKE 0138952), **MH758485, MH770986, MH770216, MH770473, MH769972, MH770777; *P. canina*** (L.) Willd. **2,** U.S.A.: NC, *Goffinet 4755* (DUKE), –, **MH770987, MH770217, MH770474,** –, **MH770778; *P. canina*** (L.) Willd. **2,** Canada: AB, *Miadlikowska & Lutzoni s.n.* (DUKE 0401817), **MH758468, MH770988, MH770218,** –, **MH769973, MH770779; *P. canina*** (L.) Willd. **2,** U.S.A.: UT, *Truong 3996* (DUKE 0401865), **MH758486, MH770989, MH770219, MH770475, MH769974, MH770780; *P. canina*** (L.) Willd. **2,** U.S.A.:

Appendix 1. Continued.

CO, *Leavitt SDL-CO-13* (BRY-C), **MH758487, MH770990, MH770220,** –, **MH769975, MH770781; *P. canina*** (L.) Willd. **2,** U.S.A.: MI, *Miadlikowska & Lutzoni s.n.* (DUKE 0401826), **MH758488, MH770991, MH770221, MH770476, MH769976, MH770782; *P. canina*** (L.) Willd. **2,** U.S.A.: TN, *Chen & Gajdeczka s.n.* (DUKE 0401818), **MH758489, MH770992, MH770222, MH770477, MH769977, MH770783; *P. castanea*** Goward & al., Russia: Krasnoyarsk Territory, *Miadlikowska & Lutzoni s.n.* (DUKE 0357981), **MH758239,** –, **MH770029, MH770279,** –, **MH770534; *P. cinnamomea*** Goward, Canada: BC, *O'Brien 030611-0-0-4* (DUKE), FJ708912, FJ709306, **MH770129, MH770394, MH769886,** –; ***P. cinnamomea*** Goward, Canada: BC, *O'Brien 040605-11-2* (DUKE), FJ708913, FJ709307, **MH770130, MH770395, MH769887,** –; ***P. cinnamomea*** Goward, Canada: BC, *O'Brien 040605-12-3* (DUKE), FJ708911, FJ709305, –, –, –, –; ***P. cinnamomea*** Goward, Canada: BC, *Goward s.n.* (UBC), **MH758379,** KX880187, **MH770131, MH770396, MH769888, MH770687; *P. continentalis*** Vitik., China: Ningxia, *Niu 12-0087* (Ningxia Univ.), **MH758236, MH770820, MH770026, MH770276, MH769773, MH770531; *P. continentalis*** Vitik., Russia: Krasnoyarsk Territory, *Miadlikowska & Lutzoni s.n.* (DUKE 0357965), **MH758237,** KM005807, **MH770027, MH770277, MH769774, MH770532; *P. continentalis*** Vitik., Russia: Krasnoyarsk Territory, *Miadlikowska & Lutzoni s.n.* (DUKE 0357969), **MH758238, MH770821, MH770028, MH770278, MH769775, MH770533; *P. degenii*** Gyeln. **1,** Norway, *Magain s.n.* (LG), **MH758402,** KM005828, **MH770136, MH770400, MH769890, MH770692; *P. degenii*** Gyeln. **1,** Norway, *Magain s.n.* (LG), **MH758403, MH770913, MH770137, MH770401, MH769891, MH770693; *P. degenii*** Gyeln. **1,** Norway, *Magain s.n.* (LG), **MH758404, MH770914, MH770138, MH770402, MH769892, MH770694; *P. degenii*** Gyeln. **1,** Austria, *Hafellner & Miadlikowska s.n.* (DUKE 0032160), **MH758399, MH770915, MH770139, MH770403, MH769893, MH770695; *P. degenii*** Gyeln. **1,** France, *Magain s.n.* (DUKE 0401808), **MH758400, MH770916, MH770140, MH770404, MH769894,** –; ***P. degenii*** Gyeln. **1,** France, *Magain s.n.* (DUKE 0401807), **MH758401, MH770917, MH770141, MH770405, MH769895, MH770696; *P. degenii*** Gyeln. **1,** Ukraine, *Dymytrova & Naumovich 183* (KW 69499), **MH758405, MH770918, MH770142, MH770406, MH769896,** –; ***P. degenii*** Gyeln. **1,** Ukraine, *Dymytrova & Savchyn 22* (KW), **MH758406, MH770919, MH770143, MH770407, MH769897, MH770697; *P. degenii*** Gyeln. **2a,** Canada: BC, *O'Brien 040605-10-3* (DUKE), FJ709030, FJ709315, **MH770144, MH770408, MH769898,** –; ***P. degenii*** Gyeln. **2a,** Canada: QC, *Darnajoux s.n.* (DUKE 0401806), **MH758410, MH770920, MH770145,** –, **MH769899, MH770698; *P. degenii*** Gyeln. **2a,** Russia: Khabarovsk Territory, *Miadlikowska & Lutzoni s.n.* (DUKE 0401824), **MH758413, MH770921, MH770146, MH770409, MH769900, MH770699; *P. degenii*** Gyeln. **2a,** Canada: BC, *Goward 02-380* (ACC L41345), **MH758407, MH770922, MH770147,** –, **MH769901, MH770700; *P. degenii*** Gyeln. **2a,** Canada: QC, *Roy 11-5914C* (QFA 0595636), **MH758411,** –, **MH770148,** –, **MH769902, MH770701; *P. degenii*** Gyeln. **2a,** Canada: QC, *Miadlikowska & Lutzoni 07.04.03-1A* (DUKE 0401805), **MH758412, MH770923, MH770149,** –, **MH769903, MH770702; *P. degenii*** Gyeln. **2a,** Japan: Hokkaido, *Thor 13948* (UPS 392189), **MH758409, MH770924, MH770150, MH770410, MH769904, MH770703; *P. degenii*** Gyeln. **2b,** Japan: Honshu, *Thor 11963* (UPS 395916), **MH758408,** –, **MH770151, MH770411, MH769905, MH770704; *P. degenii*** Gyeln. **3a,** Russia: Sakhalin, *Tchabanenko s.n.* (SAKH 3083), **MH758419, MH770925, MH770152, MH770412, MH769906, MH770705; *P. degenii*** Gyeln. **3a,** Russia: Sakhalin, *Tchabanenko s.n.* (SAKH 3081), **MH758420, MH770926, MH770153, MH770413, MH769907, MH770706; *P. degenii*** Gyeln. **3b,** China: Jilin, *Sohrabi 16474* (H), **MH758414, MH770927, MH770154, MH770414, MH769908, MH770707; *P. degenii*** Gyeln. **3b,** China: Jilin, *Sohrabi 16417* (H), **MH758415, MH770928, MH770155, MH770415, MH769909, MH770708; *P. degenii*** Gyeln. **3b,** Russia: Kurile Islands, *Abrahamczyk 15* (H), **MH758416, MH770929, MH770156, MH770416, MH769910, MH770709; *P. degenii*** Gyeln. **3c,** Japan: Honshu, *Sérusiaux s.n.* (LG), **MH758417, MH770930, MH770157, MH770417, MH769911, MH770710; *P. degenii*** Gyeln. **3c,** Japan: Honshu, *Ohmura & al. s.n.* (DUKE 0188055), **MH758418, MH770931, MH770158, MH770418, MH769912, MH770711; *P. didactyla*** (With.) J.R.Laundon **1,** Belgium, *Magain s.n.* (DUKE 0357985), **MH758240,** –, **MH770030, MH770280, MH769777, MH770535; *P. didactyla*** (With.) J.R.Laundon **1,** Norway, *Magain s.n.* (LG), **MH758244,** –, **MH770031, MH770281, MH769778,** –; ***P. didactyla*** (With.) J.R.Laundon **1,** New Zealand, Campbell Island, *Harris 5326* (NY) , **MH758241,** –, –, –, –, **MH770536; *P. didactyla*** (With.) J.R.Laundon **1,** U.S.A.: UT; *Truong 3991* (DUKE 0401851), **MH758246,** –, **MH770032, MH770282, MH769779, MH770537; *P. didactyla*** (With.) J.R.Laundon **2,** China: Sichuan, *Wang 10-31861* (KUN), **MH758243,** –, **MH770033, MH770283,** –, **MH770538; *P. didactyla*** (With.) J.R.Laundon **2,** Russia: Khabarovsk, *Miadlikowska & Lutzoni. s.n.* (DUKE 0357977), –, –, –, –, –, **MH770539; *P. didactyla*** (With.) J.R.Laundon **3,** U.S.A.: PA, *Lendemer 13269* (DUKE 0154812), **MH758245,** –, –, –, **MH769776, MH770540; *P. didactyla*** (With.) J.R.Laundon **3,** Canada: BC, *Goward s.n.* (DUKE 0017197), **MH758242,** –, **MH770034,** –, –, **MH770541; *P. erioderma*** Vain. **1,** Papua New Guinea, *Sérusiaux s.n.* (LG), **MH758380, MH770911, MH770132, MH770397, MH769889, MH770688; *P. erioderma*** Vain. **2,** Papua New Guinea, *Sérusiaux 14107* (LG), **MH758381,** –, **MH770133, MH770398,** –, **MH770689; *P. evansiana*** Gyeln., U.S.A.: NC, *Miadlikowska & al. s.n.* (DUKE 0401810), **MH758490,** –, –, –, –, **MH770784; *P. evansiana*** Gyeln., U.S.A.: PA, *Lendemer 17422* (NY 01105603), **MH758491,** KM005808, –, **MH770478, MH769978, MH770785; *P. evansiana*** Gyeln., U.S.A.: PA, *Lendemer 17753* (NY 01103610), **MH758492,** KM005809, –, –, –, –; ***P. evansiana*** Gyeln., U.S.A.: NC, *Miadlikowska & Lutzoni s.n.* (DUKE 0357991), **MH758493, MH770993, MH770225, MH770479, MH769979, MH770786; *P. evansiana*** Gyeln., U.S.A.: MI, *Miadlikowska & al s.n.* (DUKE 0401813), **MH758494, MH770994, MH770226, MH770480, MH769980, MH770787; *P. extenuata*** (Nyl. ex Vain.) Lojka **1,** Russia: Kamchatka, *Himelbrandt s.n.* (H), **MH758251,** –, –, –, –, **MH770542; *P. extenuata*** (Nyl. ex Vain.) Lojka **1,** Canada: BC, *Goward 10-74* (UBC), **MH758250,** –, –, –, –, **MH770543; *P. extenuata*** (Nyl. ex Vain.) Lojka **1,** Chile: Region XI, *Wheeler & Nelson 6297* (CONC), **MH758247,** –, **MH770035, MH770284, MH769780, MH770544; *P. extenuata*** (Nyl. ex Vain.) Lojka **1,** Russia: Krasnoyarsk Territory, *Miadlikowska & Lutzoni s.n.* (DUKE 0357970), **MH758252,** –, **MH770036, MH770285, MH769781, MH770545; *P. extenuata*** (Nyl. ex Vain.) Lojka **1,** U.S.A.: MI, *Miadlikowska & Lutzoni s.n.* (DUKE 0357972), **MH758253,** –, **MH770037, MH770286, MH769782, MH770546; *P. extenuata*** (Nyl. ex Vain.) Lojka **1,** U.S.A.: NY, *Harris 53633* (DUKE 0138925), **MH758254,** –, **MH770038, MH770287, MH769783, MH770547; *P. extenuata*** (Nyl. ex Vain.) Lojka **2,** Colombia, *Lücking 33627* (UDBC), **MH758248,** –, **MH770039, MH770288, MH769784, MH770548; *P. extenuata*** (Nyl. ex Vain.) Lojka **2,** Ecuador: Galapagos, *Spielmann 10611* (CDS-51978), **MH758249,** –, **MH770040, MH770289, MH769785, MH770549; *P. fimbriata*** Vitik. & al., Papua New Guinea, Sérusiaux & al. 2009, FJ527272, –, –, –, –, –; ***P. fimbriata***Vitik. & al., Papua New Guinea, Sérusiaux & al. 2009, FJ527273, –, –, –, –, –; ***P. fimbriata*** Vitik. & al., Papua New Guinea, Sérusiaux & al. 2009, FJ527274 , –, –, –, –, –; ***P. friesiorum*** Gyeln., Brazil, *Marcelli 25096* (H), **MH758323,** –, –, –, –, **MH770621; *P. friesiorum*** Gyeln., Brazil, *Miadlikowska & al. s.n.* (CGMS 34533), **MH758324,** –, –, –, –, **MH770622; *P. friesiorum*** Gyeln., Brazil, *Miadlikowska & al. s.n.* (CGMS 34582), **MH758325,** –, –, –, –, **MH770623; *P. friesiorum*** Gyeln., Brazil, *Miadlikowska & al. s.n.* (CGMS 34531), **MH758326,** –, –, –, –, **MH770624; *P. friesiorum*** Gyeln., Brazil, *Miadlikowska & al. s.n.* (CGMS 34575), **MH758327,** –, –, –, –, **MH770625; *P. friesiorum*** Gyeln., Brazil, *Miadlikowska & al. s.n.* (CGMS 34539), **MH758328, MH770870, MH770094, MH770351, MH769848, MH770626; *P. friesiorum*** Gyeln., Peru, *Miadlikowska s.n.* (DUKE 0401814), **MH758337, MH770872, MH770096, MH770353, MH769850, MH770628; *P. friesiorum*** Gyeln., Brazil, *Miadlikowska & al. s.n.* (CGMS 35043), **MH758330,** –, –, –, –, **MH770629; *P. friesiorum*** Gyeln., Brazil, *Lutzoni & al. s.n.* (CGMS 34570), **MH758331, MH770873,** –, –, –, **MH770630; *P. friesiorum*** Gyeln., Brazil, *Miadlikowska & al. s.n.* (CGMS 34587), **MH758332, MH770874, MH770097, MH770354, MH769851, MH770631; *P. friesiorum*** Gyeln., Brazil, *Miadlikowska & al. s.n.* (CGMS 35050), **MH758333,** –, –, –, –, **MH770632; *P. friesiorum*** Gyeln., Brazil, *Miadlikowska & al. s.n.* (CGMS 35054), **MH758334,** –, –, –, –, **MH770633; *P. friesiorum*** Gyeln., Brazil, *Spielmann & al. 9935* (CGMS 35048), **MH758335, MH770875, MH770098, MH770355, MH769852, MH770634; *P. friesiorum*** Gyeln., Bolivia, *Kukwa 8465* (ex UGDA-L-17699 DUKE dupl.), **MH758322, MH770876, MH770099, MH770356, MH769853, MH770635; *P. frigida*** R.Sant., Chile: Region XI, *Rubio 4064* (H), **MH758221,** –, –, –, –, **MH770517; *P. frigida*** R.Sant., Chile: Region XII, *Stenroos 2192* (H), **MH758222, MH770815,** –, **MH770262, MH769762, MH770518; *P. frigida*** R.Sant., Argentina, *Stenroos 2158* (H), **MH758220, MH770816, MH770016, MH770263, MH769763, MH770519; *P. frigida*** R.Sant., Chile: Region XII *Goffinet 6643-1* (CONN), –, –, –, –, –, **MH770520; *P. frigida*** R.Sant., Chile: Region XII, *Shaw 18024* (DUKE), **MH758223,** –, **MH770017, MH770264, MH769764, MH770521; *P. "fuscopraetextata",*** Canada: BC, *O'Brien 020708-62-5-3* (DUKE), FJ708893, FJ709317, **MH770175, MH770436, MH769930,** –; ***P. "fuscopraetextata",*** Canada: BC, *O'Brien 020708-31-5-3* (DUKE), FJ708892, FJ709316, **MH770176, MH770437, MH769931,** –; ***P. "fuscopraetextata",*** Canada: BC, *Goward 06-1538B* (UBC), **MH758507, MH770947, MH770177,** –, **MH769932, MH770723;**

Appendix 1. Continued.

P. "fuscopraetextata", Argentina, *Stenroos 2235* (H), **MH758500, MH770948, MH770178, MH770438, MH769933, MH770724; *P. "fuscopraetextata",*** Chile: Region XI, *Rubio 4067* (H), **MH758503, MH770949, MH770179, MH770439, MH769934, MH770725; *P. "fuscopraetextata",*** Argentina, *Tibell 17537* (UPS 40375), **MH758501,** –, –, –, –, **MH770726; *P. "fuscopraetextata",*** Chile: Region XII, *Tibell 17788* (UPS 45291), **MH758504,** –, –, –, –, **MH770727; *P. "fuscopraetextata",*** Argentina, *Kalb s.n.* (DUKE 0401830), **MH758502, MH770950, MH770180,** –, **MH769935, MH770728; *P. "fuscopraetextata",*** Chile: Region XII, *Goffinet 10490* (CONN), **MH758505, MH770951, MH770181, MH770440, MH769936, MH770729; *P. "fuscopraetextata",*** Chile: Region XII, *Wheeler & Nelson 6528* (CONC), **MH758506, MH770952, MH770182, MH770441, MH769937, MH770730; *P. "fuscopraetextata",*** U.S.A.: OR, *McCune 30990* (OSC), **MH758508,** –, **MH770183, MH770442, MH769938, MH770731; *P. "fuscopraetextata",*** U.S.A.: UT, *Truong 4016* (DUKE 0401863), **MH758509, MH770953, MH770184, MH770443, MH769939, MH770732; *P. granulosa*** Sérus. & al., Papua New Guinea, *Sérusiaux 15150* (LG), **MH758338, MH770877, MH770100, MH770357, MH769854, MH770637; *P. hymenina*** (Ach.) Delise, Canada: NL, *Lendemer 10397* (H), –, KX880099, MF947046, MF946937, MF946831 , –; ***P. isidiophora*** L.F.Han & S.Y.Guo, China: Hebei, Han & al. 2015, KJ095108, –, –, –, –, –; ***P. isidiophora*** L.F.Han & S.Y.Guo, China: Hebei, Han & al. 2015, KJ095106, –, –, –, –, –; ***P. isidiophora*** L.F.Han & S.Y.Guo, China: Hebei, Han & al. 2015, KJ095107, –, –, –, –, –; ***P. islandica*** T.Goward & S.S.Manoharan-Basil, Iceland, *Andresson 332* (AMNH), KJ413245, KJ413189, **MH770227, MH770481, MH769981,** –; ***P. islandica*** T.Goward & S.S.Manoharan-Basil, Iceland, *Manoharan-Basil 355* (AMNH), KJ413244, KJ413192, **MH770228, MH770482, MH769982,** –; ***P. kristinssonii*** Vitik., Canada: BC, *O'Brien 020708-62-1-5* (DUKE), FJ708952, FJ709345, **MH770018, MH770265,** –, –; ***P. kristinssonii*** Vitik., Canada: BC, *O'Brien 020708-70-5-9* (DUKE), FJ708944, FJ709341, **MH770019, MH770266, MH769765,** –; ***P. kristinssonii*** Vitik., Canada: BC, *Goward 11-16* (UBC), **MH758224,** –, **MH770020, MH770267, MH769766, MH770522; *P. kristinssonii*** Vitik., Canada: QC, *Gagnon s.n.* (QFA-0594989), **MH758225,** KM005796, **MH770021, MH770268, MH769767, MH770523; *P. laciniata*** (G.Merr.) Gyeln. **1,** Costa Rica, *Miadlikowska & Lutzoni 23-03-03-9* (DUKE 0401843), **MH758343,** KM005815, **MH770101, MH770358, MH769855, MH770638; *P. laciniata*** (G.Merr.) Gyeln. **1,** Costa Rica, *Miadlikowska & Lutzoni 23-03-03-23* (DUKE 0401841), **MH758344,** –, –, –, –, **MH770639; *P. laciniata*** (G.Merr.) Gyeln. **1,** Bolivia, *Kukwa 9194* (ex UGDA-L-17705, DUKE dupl. 0401840) , **MH758339,** –, –, –, –, **MH770640; *P. laciniata*** (G.Merr.) Gyeln. **1,** Ecuador, *Yanez-Anabaca 2556* (CDF), **MH758347, MH770878, MH770102, MH770359, MH769856, MH770641; *P. laciniata*** (G.Merr.) Gyeln. **1,** Colombia, *Lücking 33693* (UDBC), **MH758341, MH770879, MH770103, MH770360, MH769857, MH770642; *P. laciniata*** (G.Merr.) Gyeln. **1,** Colombia, *Coca and Patino s.n.* (FAUC), **MH758342,** –, –, –, –, **MH770643; *P. laciniata*** (G.Merr.) Gyeln. **1,** Ecuador, *Truong 3956* (DUKE 0401842), **MH758350, MH770880, MH770104, MH770361, MH769858, MH770644; *P. laciniata*** (G.Merr.) Gyeln. **1,** Ecuador, *Truong 3958* (DUKE 0401838), **MH758351,** –, –, –, –, **MH770645; *P. laciniata*** (G.Merr.) Gyeln. **2,** Bolivia, *Kukwa 9562* (ex UGDA-L-17724, DUKE dupl. 0401839), **MH758340, MH770881, MH770105, MH770362, MH769859, MH770646; *P. lepidophora*** (Vain.) Bitter **1,** Canada: BC, *Goward s.n.* (UBC), **MH758354,** KM005810, –, **MH770363, MH769860, MH770647; *P. lepidophora*** (Vain.) Bitter **1,** Iceland, *Kristinsson 49244* (AMNH LA-29491), **MH758353, MH770882, MH770106, MH770364, MH769861, MH770648; *P. lepidophora*** (Vain.) Bitter **1** , U.S.A.: NY, *Lendemer 12047* (NY 0154474), **MH758355, MH770883, MH770107, MH770365, MH769862, MH770649; *P. lepidophora*** (Vain.) Bitter **2,** U.S.A.: AK, *Miadlikowska & Lutzoni s.n.* (DUKE 0357968), **MH758352, MH770884, MH770108, MH770366, MH769863, MH770650; *P. lepidophora*** (Vain.) Bitter **2** , China: Ningxia, *Niu 12-0085* (Ningxia Univ.), **MH758356,** –, –, –, –, **MH770651; *P. malacea*** (Ach.) Funck, U.S.A.: AK, *Berg 3072* (UBC), –, **MH771011, MH770255, MH770506,** –, –; ***P. membranacea*** (Ach.) Nyl. **1,** Canada: BC, *O'Brien 040605-10-1-1* (DUKE), FJ709034, FJ709434, **MH770159, MH770419, MH769913,** –; ***P. membranacea*** (Ach.) Nyl. **1,** Canada: BC, *O'Brien 040605-1-2* (DUKE), KC437646, FJ709435, –, –, –, –; ***P. membranacea*** (Ach.) Nyl. **1,** Canada: BC, *O'Brien 020708-0-9-1* (DUKE), FJ709031, FJ709431, **MH770160, MH770420, MH769914,** –; ***P. membranacea*** (Ach.) Nyl. **1,** Iceland, *Miadlikowska & Lutzoni s.n.* (DUKE 0357981), **MH758426,** KM005814, **MH770161, MH770421, MH769915,** KX923102; ***P. membranacea*** (Ach.) Nyl. **1,** Spain, *Vare L1807* (H), **MH758431, MH770932, MH770162, MH770422, MH769916, MH770712; *P. membranacea*** (Ach.) Nyl. **1,** Norway, *Magain s.n.* (LG), **MH758428, MH770933,** –, **MH770423, MH769917, MH770713; *P. membranacea*** (Ach.) Nyl. **1,** Canada: BC, *Truong s.n.* (DUKE 0401833), **MH758421, MH770934, MH770163, MH770424, MH769918, MH770714; *P. membranacea*** (Ach.) Nyl. **1,** Portugal, *Vust 3084* (G), **MH758429, MH770935, MH770164, MH770425, MH769919, MH770715; *P. membranacea*** (Ach.) Nyl. **1,** France: Corsica, *Vust 6423* (G), **MH758422, MH770936, MH770165, MH770426, MH769920, MH770716; *P. membranacea*** (Ach.) Nyl. **1,** France: Corsica, *Vust 6405* (G), **MH758423, MH770937, MH770166, MH770427, MH769921,** –; ***P. membranacea*** (Ach.) Nyl. **1,** France, *Magain s.n.* (DUKE 0401819), **MH758424, MH770938, MH770167, MH770428, MH769922,** –; ***P. membranacea*** (Ach.) Nyl. **1,** Iceland, *Heidmarsson 2746* (AMNH LA-31754), **MH758427, MH770939, MH770168, MH770429, MH769923, MH770717; *P. membranacea*** (Ach.) Nyl. **1,** Greenland, *Vust 6432* (G), **MH758425,** –, –, –, –, –; ***P. membranacea*** (Ach.) Nyl.**2,** Russia: Khabarovsk Territory, *Miadlikowska & al. s.n.* (DUKE 0401812), **MH758430, MH770940, MH770169, MH770430, MH769924,** –; ***P. montis-wilhelmii*** Sérus. & al. **1,** Papua New Guinea, *Sérusiaux s.n.* (LG), **MH758382, MH770912, MH770134, MH770399,** –, **MH770690; *P. montis-wilhelmii*** Sérus. & al. **2,** Papua New Guinea, *Sérusiaux 13984* (LG), **MH758383,** –, **MH770135,** –, –, **MH770691; *P. "neocanina"* 1,** Canada: BC, *O'Brien 020708-0-5-1* (DUKE), FJ708922, FJ709443, –, –, –, –; ***P. "neocanina"* 1,** Canada: BC, *O'Brien 020708-66-5-2* (DUKE), FJ708916, FJ709444, –, –, –, –; ***P. "neocanina"* 1,** Canada:BC, *O'Brien 020708-66-9-1* (DUKE), FJ708917, FJ709438, –, **MH770382,** –, –; ***P. "neocanina"* 1,** Canada: BC, *O'Brien 040605-2-2* (DUKE), KC437635, **MH770899, MH770120, MH770383, MH769875,** KC437877; ***P. "neocanina"* 1,** U.S.A.: NM, *Hollinger 2460* (UBC), **MH758395, MH770900,** –, –, –, KX923107; ***P. "neocanina"* 1,** Canada: BC, *Goward 11-37* (UBC), **MH758388,** –, –, –, –, **MH770672; *P. "neocanina"* 1,** Canada: MB, *Ahti 63078* (H), –, –, –, –, –, **MH770673; *P. "neocanina"* 1,** U.S.A.: NM, *Hollinger 2402* (UBC), **MH758396,** –, –, –, –, **MH770674; *P. "neocanina"* 1,** U.S.A.: AK, *Miadlikowska & Lutzoni s.n.* (DUKE 0401834), **MH758384, MH770901, MH770121, MH770384, MH769876, MH770675; *P. "neocanina"* 1,** U.S.A.: AK, *Miadlikowska & Lutzoni s.n.* (DUKE 0401816), –, **MH770902, MH770122, MH770385, MH769877, MH770676; *P. "neocanina"* 1,** Canada: BC, *Goward 5306* (UBC), **MH758385, MH770903, MH770123, MH770386, MH769878, MH770677; *P. "neocanina"* 2,** U.S.A.: NM, *Hollinger 2401* (UBC), **MH758394, MH770904, MH770124, MH770387, MH769879,** KX923106; ***P. "neocanina"* 2,** U.S.A.: CO, *King L286* (NY), **MH758397, MH770905,** –, **MH770388, MH769880, MH770678; *P. "neocanina"* 2,** U.S.A.: UT, *Truong 3995* (DUKE 0401867), **MH758398, MH770906, MH770125, MH770389, MH769881, MH770679; *P. "neocanina"* 3,** Russia: Krasnoyarsk Territory, *Miadlikowska & al. s.n.* (DUKE 0401821), **MH758390, MH770907,** –, **MH770390, MH769882, MH770680; *P. "neocanina"* 3,** Russia: Krasnoyarsk Territory, *Miadlikowska s.n.* (DUKE 0401802), **MH758391,** –, –, –, –, **MH770681; *P. "neocanina"* 3,** Russia: Krasnoyarsk Territory, *Miadlikowska s.n.* (DUKE 0401801), **MH758392,** –, –, –, –, **MH770682; *P. "neocanina"* 3,** Russia: Krasnoyarsk Territory, *Miadlikowska s.n.* (DUKE 0401803), **MH758393,** –, –, –, –, **MH770683; *P. "neocanina"* 3,** China: Yunnan, *Goffinet 9979* (CONN), **MH758386, MH770908, MH770126, MH770391, MH769883, MH770684; *P. "neocanina"* 4,** Iceland, *Miadlikowska & Lutzoni 08.08.10-5* (DUKE 0401832), **MH758387, MH770909, MH770127, MH770392, MH769884, MH770685; *P. "neocanina"* 4,** Norway, *Goward 02-1480* (UBC), **MH758389, MH770910, MH770128, MH770393, MH769885, MH770686; *P. "neorufescens"* 1,** Mexico, *Barcenas-Peña 1229* (MEXU), **MH758362, MH770862, MH770088, MH770343, MH769840, MH770614; *P. "neorufescens"* 1,** Costa Rica, *Miadlikowska & al. s.n.* (DUKE 0401820), **MH758360, MH770863, MH770089, MH770344, MH769841, MH770613; *P. "neorufescens"* 2,** Bolivia, *Kukwa 8958* (ex UGDA-L-17704, DUKE dupl. 0401871), **MH758357, MH770864, MH770090, MH770345, MH769842, MH770614; *P. "neorufescens"* 2,** Peru, *Bennett s.n.* (WIS), **MH758363, MH770865, MH770091, MH770346, MH769843, MH770615; *P. "neorufescens"* 3,** Germany, Sipman 53601 (B 600127393), **MH758361, MH770866, MH770092, MH770347, MH769844, MH770616; *P. "neorufescens"* 4,** Canada: AB, *Miadlikowska & Lutzoni s.n.* (DUKE 0401823), **MH758359, MH770867, MH770093, MH770348, MH769845, MH770617; *P. "neorufescens"* 5,** Canada: YT, *Lendemer 28945* (NY 0159332), **MH758358, MH770868,** –, **MH770349, MH769846, MH770618; *P. "neorufescens"* 6,** U.S.A.: UT, *Truong 4023* (DUKE 0401868), **MH758364, MH770869,** –, **MH770350, MH769847, MH770619; *P. "neorufescens"* 6,** U.S.A.: OR, *Stone 8083.1* (DUKE 0158517), **MH758365,** –, –, –, –, **MH770620; *P. papuana*** Sérus. & al., Papua New Guinea, *Sérusiaux 13656* (LG), –, –, –, –, –, **MH770652; *P. papuana*** Sérus. & al., Papua New Guinea, *Sérusiaux 13655* (LG), **MH758366, MH770885,** –, **MH770367,** –, **MH770653; *P. patagonica*** Räsänen, Chile: Region XI, *Rubio*

Appendix 1. Continued.

4077 (H), **MH758227,** –, **MH770022, MH770269, MH769768,** KX923108; ***P. patagonica*** Räsänen, Chile: Region XII, *Stenroos 2427* (H), **MH758228,** –, **MH770023, MH770270, MH769769, MH770524; *P. patagonica*** Räsänen, Chile: Region XII, *Tibell 18056* (UPS 74661), –, –, –, –, –, **MH770525; *P. patagonica*** Räsänen, Argentina, *Tibell 17450* (UPS 40293), **MH758226,** –, –, **MH770271,** –, **MH770526; *P. polydactylon*** (Neck.) Hoffm., Norway; *Magain s.n.* (LG), –, KM005765, KX365489, KX373621, KX373632, –; ***P. ponojensis*** Gyeln./***monticola*** Vitik. **1a,** U.S.A.: PA, *Lendemer 13556* (H), **MH758276, MH770833, MH770059, MH770309, MH769803,** KX923111; ***P. ponojensis*** Gyeln./***monticola*** Vitik. **1a,** Canada: BC, *Goward 7-187* (UBC), **MH758277,** –, **MH770060,** –, **MH769804, MH770571; *P. ponojensis*** Gyeln./***monticola*** Vitik. **1a,** U.S.A.: ME, *Harris 55417* (NY 01103744), **MH758278,** –, –, –, **MH769806, MH770573; *P. ponojensis*** Gyeln./***monticola*** Vitik. **1a,** Canada: MB, *Ahti 62717* (H), **MH758279, MH770834,** –, **MH770310, MH769807, MH770574; *P. ponojensis*** Gyeln./***monticola*** Vitik. **1a,** U.S.A.: MO, *Harris 48184* (NY 01180306), **MH758280, MH770835, MH770062, MH770311, MH769808, MH770575; *P. ponojensis*** Gyeln./***monticola*** Vitik. **1a,** U.S.A.: OR, *McCune 29956* (OSC), **MH758281, MH770836, MH770063, MH770312, MH769809, MH770576; *P. ponojensis*** Gyeln./***monticola*** Vitik. **1a,** Canada: AB, *Miadlikowska & Lutzoni s.n.* (DUKE 0401809), **MH758282, MH770837, MH770064, MH770313, MH769810, MH770577; *P. ponojensis*** Gyeln./***monticola*** Vitik. **1a,** Canada: BC, *Goward 07-234a* (UBC), **MH758283,** –, **MH770061,** –, **MH769805, MH770572; *P. ponojensis*** Gyeln./***monticola*** Vitik. **1b,** U.S.A.: UT, *Truong 4045* (DUKE 0401866), **MH758284, MH770838, MH770065, MH770314, MH769811, MH770578; *P. ponojensis*** Gyeln./***monticola*** Vitik. **2,** Germany, *Türk 34539* (H), **MH758285, MH770839,** –, **MH770315, MH769812, MH770579; *P. ponojensis*** Gyeln./***monticola*** Vitik. **2,** France, *Magain s.n.* (LG), **MH758286, MH770840, MH770066, MH770316, MH769813,** –; ***P. ponojensis*** Gyeln./***monticola*** Vitik. **2,** Switzerland, *Vust 1687* (G), **MH758287, MH770841, MH770067, MH770317, MH769814, MH770580; *P. ponojensis*** Gyeln./***monticola*** Vitik. **3,** Canada: BC, *O'Brien 020708-62-1-3* (DUKE), FJ709039, FJ709448, –, –, –, –; ***P. ponojensis*** Gyeln./***monticola*** Vitik. **4,** U.S.A.: KS, *Buck 46381* (NY 881403), **MH758288, MH770842,** –, **MH770318, MH769815, MH770581; *P. ponojensis*** Gyeln./***monticola*** Vitik. **4,** U.S.A.: MO, *Harris 45692* (NY), **MH758289, MH770843, MH770068, MH770319, MH769816, MH770582; *P. ponojensis*** Gyeln./***monticola*** Vitik. **4,** U.S.A.: AR, *Buck 46600* (NY 0050439), **MH758290, MH770844, MH770069, MH770320, MH769817, MH770583; *P. ponojensis*** Gyeln./***monticola*** Vitik. **4,** U.S.A.: AR, *Majestyk 8060* (DUKE 0401845), **MH758291, MH770845, MH770070, MH770321, MH769818, MH770584; *P. ponojensis*** Gyeln./***monticola*** Vitik. **5a,** India: Uttarakhand, *Divakar s.n.* (MAF), **MH758293, MH770846, MH770071, MH770322, MH769819, MH770585; *P. ponojensis*** Gyeln./***monticola*** Vitik. **5a,** China: Yunnan, *Rosentreter 15* (DUKE 0401846), **MH758292, MH770847, MH770072, MH770323, MH769820, MH770586; *P. ponojensis*** Gyeln./***monticola*** Vitik. **5b,** Canada: BC, *O'Brien 020708-70-1-4* (DUKE), FJ709040, FJ709449, –, **MH770324, MH769821,** –; ***P. ponojensis*** Gyeln./***monticola*** Vitik. **6,** China: Ningxia, *Niu 12-0015* (Ningxia Univ.), –, –, –, –, –, **MH770587; *P. ponojensis*** Gyeln./***monticola*** Vitik. **6,** China: Ningxia, *Niu 12-0016* (Ningxia Univ.), –, –, –, –, –, **MH770588; *P. ponojensis*** Gyeln./***monticola*** Vitik. **6,** Norway, *Magain s.n.* (LG), **MH758294,** –, –, **MH770325, MH769822,** –; ***P. ponojensis*** Gyeln./***monticola*** Vitik. **6,** China: Yunnan, *Miadlikowska s.n.* (DUKE 0401815), **MH758295, MH770848,** –, **MH770326, MH769823, MH770589; *P. ponojensis*** Gyeln./***monticola*** Vitik. **7,** Norway, *Ahti 65831* (H), **MH758296,** KM005825, **MH770073, MH770327, MH769824,** KX923104; ***P. ponojensis*** Gyeln./***monticola*** Vitik. **7,** U.S.A.: CA, *McCune 30357* (OSC) , **MH758297, MH770849, MH770074, MH770328, MH769825, MH770590; *P. ponojensis*** Gyeln./***monticola*** Vitik. **8,** U.S.A.: UT, *Buck 55054* (NY01136425), **MH758298, MH770850, MH770075, MH770329, MH769826, MH770591; *P. ponojensis*** Gyeln./***monticola*** Vitik. **8,** Canada: BC, *Goward 5302* (UBC), **MH758299, MH770851, MH770076, MH770330, MH769827, MH770592; *P. ponojensis*** Gyeln./***monticola*** Vitik. **8,** U.S.A.: UT, *Truong 4048* (DUKE 040189), **MH758300,** –, **MH770077, MH770331, MH769828, MH770593; *P. ponojensis*** Gyeln./***monticola*** Vitik. **8,** U.S.A.: UT; *Truong 4027* (DUKE 0401847), **MH758301,** –, –, –, –, **MH770594; *P. ponojensis*** Gyeln./***monticola*** Vitik. **8,** U.S.A.: UT, *Truong 4001* (DUKE 0401848), **MH758302, MH770852, MH770078, MH770332, MH769829, MH770595; *P. ponojensis*** Gyeln./***monticola*** Vitik. **8,** U.S.A.: UT, *Truong 4011* (DUKE 0401850), **MH758303,** –, –, –, –, **MH770596; *P. ponojensis*** Gyeln./***monticola*** Vitik. **8,** Canada: BC, *Goward 5300* (UBC), **MH758305, MH770853, MH770079, MH770333, MH769830, MH770597; *P. ponojensis*** Gyeln./***monticola*** Vitik. **8,** U.S.A.: OR, *Hardman s.n.* (DUKE 0158521), **MH758304, MH770854, MH770080, MH770334, MH769831, MH770598; *P. ponojensis*** Gyeln./***monticola*** Vitik. **9,** China: Ningxia, *Niu 12-0005* (Ningxia Univ.), **MH758307, MH770855, MH770081, MH770335, MH769832, MH770599; *P. ponojensis*** Gyeln./***monticola*** Vitik. **9,** China: Ningxia, *Niu 12-0004* (Ningxia Univ.), **MH758306,** –, –, –, –, **MH770600; *P. ponojensis*** Gyeln./***monticola*** Vitik. **9,** Austria, *Türk 37593* (H), **MH758310,** KM005824, **MH770082, MH770336, MH769833,** KX923103; ***P. ponojensis*** Gyeln./***monticola*** Vitik. **9,** Russia: Dagestan, *Urbanavichus 0902150* (H), **MH758308, MH770856,** –, **MH770337, MH769834, MH770590; *P. ponojensis*** Gyeln./***monticola*** Vitik. **9,** Switzerland, *Vust s.n*. (G), **MH758309, MH770857, MH770083, MH770338, MH769835, MH770591; *P. ponojensis*** Gyeln./***monticola*** Vitik. **10a,** U.S.A.: CA, *Arnold 73* (YOSE 221393), **MH758311, MH770829,** –, **MH770305, MH769799, MH770567; *P. ponojensis*** Gyeln./***monticola*** Vitik. **10a,** U.S.A.: CA, *McCune 28024* (OSC) , **MH758313, MH770830, MH770056, MH770306, MH769800, MH770568; *P. ponojensis*** Gyeln./***monticola*** Vitik. **10a,** U.S.A.: CA, *McCune 29670* (OSC) , **MH758314, MH770831, MH770057, MH770307, MH769801, MH770569; *P. ponojensis*** Gyeln./***monticola*** Vitik. **10b,** U.S.A.: UT, *Truong & Magain s.n.* (DUKE 0357983), **MH758312, MH770832, MH770058, MH770308, MH769802, MH770570; *P. praetextata*** (Flörke ex Sommerf.) Zopf, Canada: BC, *O'Brien 030611-0-0-5* (DUKE), FJ708905, FJ709451, **MH770229, MH770483, MH769983,** –; ***P. praetextata*** (Flörke ex Sommerf.) Zopf, Canada: BC, *O'Brien 020708-31-9-2* (DUKE), FJ708904, FJ709450, **MH770230, MH770484, MH769984,** –; ***P. praetextata*** (Flörke ex Sommerf.) Zopf, Canada: BC, *O'Brien 030611-0-5-8* (DUKE), FJ708906, FJ709452, –, –, –, –; ***P. praetextata*** (Flörke ex Sommerf.) Zopf, Serbia, *Uotila 48419* (H), **MH758520,** –, –, –, **MH769985, MH770788; *P. praetextata*** (Flörke ex Sommerf.) Zopf, Norway, *Magain s.n.* (LG), **MH758515,** KM005829, **MH770231, MH770485, MH769986, MH770789; *P. praetextata*** (Flörke ex Sommerf.) Zopf, Norway, *Magain s.n.* (LG), **MH758516, MH770995, MH770232, MH770486, MH769987,** –; ***P. praetextata*** (Flörke ex Sommerf.) Zopf, Norway, *Magain s.n.* (LG), **MH758517,** –, –, –, –, –, **MH770790; *P. praetextata*** (Flörke ex Sommerf.) Zopf, China: Yunnan, *Miadlikowska s.n.* (DUKE 0357962), **MH758512,** –, –, –, –, **MH770791; *P. praetextata*** (Flörke ex Sommerf.) Zopf, China: Yunnan, *Miadlikowska s.n.* (DUKE 0357961), **MH758513, MH770996, MH770233, MH770487, MH769988, MH770792; *P. praetextata*** (Flörke ex Sommerf.) Zopf, Russia: Karachaevo-Cherkesiya Republic, *Zhurbenko s.n.* (DUKE 0357996), **MH758518, MH770997, MH770234, MH770488, MH769989, MH770793; *P. praetextata*** (Flörke ex Sommerf.) Zopf, U.S.A.: NY, *Buck 54040* (NY 01077051), **MH758521, MH770998, MH770235, MH770489, MH769990, MH770794; *P. praetextata*** (Flörke ex Sommerf.) Zopf, Canada: ON, *Harris 56462* (DUKE 0159321), **MH758510, MH770999, MH770236,** –, –, –; ***P. praetextata*** (Flörke ex Sommerf.) Zopf, U.S.A.: ME, *Harris 53056* (DUKE 0138948), **MH758522, MH771000, MH770237, MH770490, MH769991, MH770795; *P. praetextata*** (Flörke ex Sommerf.) Zopf, India: Himachal Pradesh, *Divakar s.n.* (MAF), **MH758514, MH771001,** –, **MH770491, MH769992, MH770796; *P. praetextata*** (Flörke ex Sommerf.) Zopf, U.S.A.: MI, *Miadlikowska & Lutzoni s.n.* (DUKE 0357993), **MH758523, MH771002, MH770238, MH770492, MH769993, MH770797; *P. praetextata*** (Flörke ex Sommerf.) Zopf, Russia: Khabarovsk Territory, *Miadlikowska & Lutzoni s.n.* (DUKE 0401831), **MH758519, MH771003, MH770239, MH770493, MH769994, MH770798; *P. praetextata*** (Flörke ex Sommerf.) Zopf, Canada: AB, J. *Miadlikowska & Lutzoni s.n.* (DUKE 0357995), **MH758511,** –, –, –, –, **MH770799; *P. praetextata*** (Flörke ex Sommerf.) Zopf, U.S.A.: AZ, *Miadlikowska & Lutzoni s.n.* (DUKE 0401835), **MH758524, MH771004, MH770240, MH770494, MH769995, MH770800; *P. retifoveata*** Vitik., Russia: Sakha Republic, *Ahti 61821* (H), **MH758213,** –, **MH770010, MH770257, MH769757, MH770508; *P. retifoveata*** Vitik., Norway, *Magain s.n.* (LG), **MH758214,** –, –, –, –, **MH770509; *P. retifoveata*** Vitik., U.S.A.: AK, *Miadlikowska & Lutzoni s.n.* (DUKE 0357984), **MH758215,** –, **MH770011, MH770258, MH769758, MH770510; *P. rufescens*** (Weiss) Humb. **1,** Canada: BC, *Goward 10-71* (UBC), **MH758369,** –, –, –, –, **MH770654; *P. rufescens*** (Weiss) Humb. **1,** Denmark, *Hansen s.n.* (H), **MH758368, MH770886,** –, **MH770368, MH769864, MH770655; *P. rufescens*** (Weiss) Humb. **1,** Chile: Region XII, *Goffinet 7076* (CONN), **MH758367, MH770887, MH770109, MH770369, MH769865, MH770656; *P. rufescens*** (Weiss) Humb. **1,** U.S.A.: NC, *Hollinger 2711* (UBC), **MH758370, MH770888, MH770110, MH770370, MH769866, MH770657; *P. rufescens*** (Weiss) Humb. **1,** U.S.A.: UT, *Truong 4044* (DUKE 0401869), –, **MH770889, MH770111, MH770371, MH769867, MH770658; *P. rufescens*** (Weiss) Humb. **2,** Costa Rica, *Miadlikowska & Lutzoni 23.03.03-3* (DUKE 0401870), **MH758371, MH770890,** –, **MH770372, MH769868, MH770659; *P. rufescentiformis***

Appendix 1. Continued.

(Gyeln.) C.W.Dodge, Kenya, *Moberg 3983* (UPS L-536565), **MH758372,** –, **MH770112, MH770373,** –, **MH770660; *P. rufescentiformis*** (Gyeln.) C.W.Dodge, Kenya, *Moberg 4324* (UPS L-536552), **MH758373, MH770891, MH770113, MH770374,** –, **MH770661; *P. scabrosa*** Th. Fr., Canada: QC, *Lutzoni & al. s.n.* (DUKE 0401873), –, KM005791, –, MF947024, MF946916, –; ***P. soredians*** Vitik., Ecuador, *Kalb 39784* (DUKE), **MH758346,** –, –, –, –, **MH770662; *P. soredians*** Vitik., Costa Rica, *Miadlikowska & Lutzoni 22.03.03-2* (DUKE 0401844), **MH758345,** –, –, –, –, **MH770663; *P. soredians*** Vitik., Ecuador, *Kalb 39787* (DUKE), **MH758348, MH770892, MH770114, MH770375,** –, **MH770664; *P. soredians*** Vitik., Ecuador, *Kalb 39785* (DUKE), **MH758349, MH770893, MH770115, MH770376, MH769869, MH770665; *P. sorediifera*** (Nyl.) Vitik., Australia, NSW, *Streimann 50996* (H), **MH758255,** –, **MH770041, MH770290, MH769786, MH770550; *P. sorediifera*** (Nyl.) Vitik., Australia: ACT, *Streimann & Curnow 34999* (ex CBG- 9507177 dupl. H), **MH758256,** –, **MH770042, MH770291,** –, **MH770551; *P.* sp. ,** China: Ningxia, *Niu 12-0064* (Ningxia Univ.), –, –, –, –, –, **MH770666; *P.* sp. 13,** China: Yunnan, *Goffinet 9974* (CONN), **MH758216,** –, **MH770012,** –, **MH769759, MH770511; *P.* sp. 14,** Chile: Region XII, *Buck 47968* (NY), **MH758217, MH770817,** –, **MH770272,** –, **MH770527; *P.* sp. 14,** Chile: Region XII, *Shaw 17848* (DUKE 0401861), **MH758218, MH770818, MH770024, MH770273, MH769770, MH770528; *P.* sp. 14,** Chile: Region X, *Wheeler & Nelson 5191* (CONC), **MH758219, MH770819,** –, **MH770274, MH769771, MH770529; *P.* sp. 15,** Ecuador, *Frisch 96/Eq101* (H), **MH758375, MH770894, MH770116, MH770377, MH769870, MH770667; *P.* sp. 15,** Colombia, *Lücking 34027* (UDBC), **MH758374, MH770895, MH770117, MH770378, MH769871, MH770668; *P.* sp. 16,** U.S.A.: OR, *McCune 31966* (OSC), **MH758235,** –, **MH770025, MH770275, MH769772, MH770530; *P.* sp. 17,** Peru, *Miadlikowska s.n.* (DUKE), **MH758316,** –, –, –, –, **MH770603; *P.* sp. 17,** Peru, *Lutzoni 05.22.2012-1* (DUKE 0357994), **MH758317,** –, –, –, –, **MH770604; *P.* sp. 17,** Peru, *Miadlikowska s.n.* (DUKE), –, –, –, –, –, **MH770605; *P.* sp. 17,** Peru, *Miadlikowska & Lutzoni s.n.* (DUKE 0357963), **MH758318,** –, –, –, –, **MH770606; *P.* sp. 17,** Peru, *Miadlikowska & Lutzoni s.n.* (DUKE 0357964), **MH758319,** –, –, –, –, **MH770607; *P.* sp. 17,** Peru, *Lutzoni 05.22.2012-8* (DUKE 0401804), **MH758320, MH770858, MH770084, MH770339, MH769836, MH770610; *P.* sp. 17,** Peru, *Miadlikowska s.n.* (DUKE 0357990), **MH758321, MH770859, MH770085, MH770340, MH769837, MH770611; *P.* sp. 17,** Peru, *Lutzoni s.n.* (DUKE 0401811), –, **MH770860, MH770086, MH770341, MH769838, MH770612; *P.* sp. 17,** Ecuador, *Truong 3976* (DUKE 0401864), **MH758315, MH770861, MH770087, MH770342, MH769839, MH770613; *P.* sp. 18,** Russia: Krasnoyarsk Territory, *Zhurbenko s.n.* (DUKE 0357978), **MH758527, MH771005, MH770241,** –, **MH769996, MH770801; *P.* sp. 18,** India: Uttarakhand, *Divakar s.n.* (MAF), **MH758526, MH771006, MH770242, MH770495, MH769997, MH770802; *P.* sp. 19,** U.S.A.: OR, *McCune 31048* (OSC), **MH758528, MH771007, MH770243, MH770496, MH769998, MH770803; *P.* sp. 19,** U.S.A.: OR, *McCune 26686* (OSC), **MH758529, MH771008, MH770244, MH770497, MH769999, MH770804; *P.* sp. 19,** U.S.A.: OR, *McCune 30122* (OSC), **MH758530, MH771009, MH770245, MH770498, MH770000, MH770805; *P.* sp. 20,** Canada: BC, *O'Brien 030611-10-0-4* (DUKE), FJ708909, FJ709455, **MH770246, MH770499, MH770001,** KC437728; ***P.* sp. 20,** Canada: BC, *O'Brien 020708-62-1-1* (DUKE), FJ708907, FJ709453, **MH770247, MH770500, MH770002,** –; ***P.* sp. 20,** Canada: BC, *O'Brien 020708-66-1-4* (DUKE), FJ708908, FJ709454, **MH770248, MH770501, MH770003,** –; ***P.* sp. 20,** Canada: BC, *O'Brien 030611-10-5-3* (DUKE), FJ708910, FJ709456, **MH770249,** –, **MH770004,** –; ***P.* sp. 21,** U.S.A.: AZ, *Miadlikowska & Lutzoni s.n.* (DUKE 0401825), **MH758525, MH771010, MH770250, MH770502, MH770005, MH770806; *P.* sp. 22,** Colombia, *Lücking MPNNC174* (UDBC), **MH758496,** –, –, –, –, **MH770808; *P.* sp. 22,** Colombia, *Lücking MPNNC122* (UDBC), **MH758495,** –, **MH770251, MH770503, MH770006, MH770807; *P.* sp. 22,** Peru, *Bennett s.n.* (WIS), **MH758498,** –, **MH770252,** –, **MH770007, MH770809; *P.* sp. 22,** Peru, *Miadlikowska s.n.* (DUKE 0357976), **MH758499,** –, **MH770253, MH770504,** –, **MH770810; *P.* sp. 22,** Colombia, *Lücking MPNNC92m* (UDBC), **MH758497,** –, **MH770254, MH770505, MH770008, MH770811; *P. spuriella*** Vain., Peru, *Maldonado 14* (NY), **MH758329, MH770871, MH770095, MH770352, MH769849, MH770627; *P. spuriella*** Vain., Peru, *Lutzoni s.n.* (DUKE), **MH758336,** –, –, –, –, **MH770636; *P. tereziana*** Gyeln., Australia: VIC, *Streimann 50914* (H), **MH758432, MH770941, MH770170, MH770431, MH769925, MH770718; *P. tereziana*** Gyeln., Australia: ACT, *Kalb 30730* (DUKE), **MH758433, MH770942, MH770171, MH770432, MH769926, MH770719; *P. tereziana*** Gyeln., New Zealand, *Tibell 9563* (UPS L-536309), **MH758437, MH770943,** –, –, –, –; ***P. tereziana*** Gyeln., Australia: NSW, *Streimann 63484* (CANB 604582.1), **MH758434, MH770944, MH770172, MH770433, MH769927, MH770720; *P. tereziana*** Gyeln., Australia: NSW, *Streimann 60382* (CBG 9906411), **MH758435, MH770945, MH770173, MH770434, MH769928, MH770721; *P. tereziana*** Gyeln., Australia: VIC, *Elix 39629* (CANB 00792024), **MH758436, MH770946, MH770174, MH770435, MH769929, MH770722; *P. ulcerata*** Müll. Arg.., Philippines, *Kalb & Schrogl s.n.* (DUKE), **MH758266,** –, –, –, –, –; ***P. ulcerata*** Müll. Arg. **1,** Costa Rica, *Miadlikowska & Lutzoni 23.03.03-24* (DUKE 0357988), **MH758262,** –, –, –, –, **MH770553; *P. ulcerata*** Müll. Arg. **1,** Costa Rica, *Miadlikowska & Lutzoni 23.03.03-26* (DUKE 0357989), **MH758263,** –, –, –, –, KX923115; ***P. ulcerata*** Müll. Arg. **1,** Costa Rica, *Miadlikowska & Lutzoni 23.03.03-31* (DUKE 0357987), **MH758264,** –, **MH770043, MH770292, MH769787, MH770554; *P. ulcerata*** Müll. Arg. **1,** Chile: Region X, *Wheeler & Nelson 5444* (CONC), **MH758259,** –, **MH770044, MH770293, MH769788, MH770555; *P. ulcerata*** Müll. Arg. **1,** Peru, *Lutzoni s.n.* (DUKE 0357986), **MH758265,** –, **MH770045, MH770294, MH769789, MH770556; *P. ulcerata*** Müll. Arg. **1,** Colombia, *Lücking DNA1190* (UDBC), **MH758260,** –, **MH770046, MH770295, MH769790, MH770557; *P. ulcerata*** Müll. Arg. **1,** Costa Rica, *Miadlikowska & Lutzoni 23-03-03-16* (DUKE 0357992), **MH758261,** –, –, –, –, **MH770552; *P. ulcerata*** Müll. Arg. **2** , Brazil: Rio, *Marcelli & al. 25096* (H), **MH758258,** –, **MH770047, MH770296, MH769791, MH770558; *P. ulcerata*** Müll. Arg. **2** , Australia: NSW, *Elix 35980* (ex CBG 9616513 dupl. H), **MH758257,** –, **MH770048, MH770297, MH769792, MH770559; *P. vainioi*** Gyeln., Colombia, *Aguirre & Sipman 5570* (B), **MH758267,** –, –, –, –, **MH770560; *P. vainioi*** Gyeln., Colombia, *Miadlikowska s.n.* (ANDES), **MH758268,** –, **MH770049, MH770298, MH769793, MH770561; *P. vainioi*** Gyeln., Ecuador, *Truong 3983* (DUKE 0401860), **MH758269,** –, **MH770050, MH770299, MH769794, MH770562; *P. wulingensis*** L.F.Han & S.Y.Guo, Canada: QC, *Gagnon s.n.* (QFA 0595019), **MH758377, MH770896,** –, **MH770379, MH769872, MH770669; *P. wulingensis*** L.F.Han & S.Y.Guo, Russia: Krasnoyarsk Territory, *Miadlikowska s.n.* (DUKE 0357978), **MH758378, MH770897, MH770118, MH770380, MH769873, MH770670; *P. wulingensis*** L.F.Han & S.Y.Guo, Canada: AB, *Miadlikowska & Lutzoni s.n.* (DUKE 0357979), **MH758376, MH770898, MH770119, MH770381, MH769874, MH770671**