Persoonia 51, 2023: 1–88
www.ingentaconnect.com/content/nhn/pimj

**RESEARCH ARTICLE**

ISSN (Online) 1878-9080
https://doi.org/10.3767/persoonia.2023.51.01

# High species richness in the lichen genus *Peltigera* (*Ascomycota, Lecanoromycetes*): 34 species in the dolichorhizoid and scabrosoid clades of section *Polydactylon*, including 24 new to science

N. Magain[1,2], J. Miadlikowska[2], B. Goffinet[3], T. Goward[4], C.J. Pardo-De la Hoz[2], I. Jüriado[5], A. Simon[1,3], J.A. Mercado-Díaz[6], T. Barlow[2], B. Moncada[7], R. Lücking[8], A. Spielmann[9], L. Canez[9], L.S. Wang[10], P. Nelson[11], T. Wheeler[12], F. Lutzoni[2], E. Sérusiaux[1]

**Key words**

cryptic species
identification key
new taxa
*Peltigerales*
species delimitation

**Abstract** Applying molecular methods to fungi establishing lichenized associations with green algae or cyanobacteria has repeatedly revealed the existence of numerous phylogenetic taxa overlooked by classical taxonomic approaches. Here, we report taxonomical conclusions based on multiple species delimitation and validation analyses performed on an eight-locus dataset that includes world-wide representatives of the dolichorhizoid and scabrosoid clades in section *Polydactylon* of the genus *Peltigera*. Following the recommendations resulting from a consensus species delimitation approach and additional species validation analysis (BPP) performed in this study, we present a total of 25 species in the dolichorhizoid clade and nine in the scabrosoid clade, including respectively 18 and six species that are new to science and formally described. Additionally, one combination and three varieties (including two new to science) are proposed in the dolichorhizoid clade. The following 24 new species are described: *P. appalachiensis*, *P. asiatica*, *P. borealis*, *P. borinquensis*, *P. chabanenkoae*, *P. clathrata*, *P. elixii*, *P. esslingeri*, *P. flabellae*, *P. gallowayi*, *P. hawaiiensis*, *P. holtanhartwigii*, *P. itatiaiae*, *P. hokkaidoensis*, *P. kukwae*, *P. massonii*, *P. mikado*, *P. nigriventris*, *P. orientalis*, *P. rangiferina*, *P. sipmanii*, *P. stanleyensis*, *P. vitikainenii* and *P. willdenowii*; the following new varieties are introduced: *P. kukwae* var. *phyllidiata* and *P. truculenta* var. *austroscabrosa*; and the following new combination is introduced: *P. hymenina* var. *dissecta*. Each species from the dolichorhizoid and scabrosoid clades is morphologically and chemically described, illustrated, and characterised with ITS sequences. Identification keys are provided for the main biogeographic regions where species from the two clades occur. Morphological and chemical characters that are commonly used for species identification in the genus *Peltigera* cannot be applied to unambiguously recognise most molecularly circumscribed species, due to high variation of thalli formed by individuals within a fungal species, including the presence of distinct morphs in some cases, or low interspecific variation in others. The four commonly recognised morphospecies: *P. dolichorhiza*, *P. neopolydactyla*, *P. pulverulenta* and *P. scabrosa* in the dolichorhizoid and scabrosoid clades represent species complexes spread across multiple and often phylogenetically distantly related lineages. Geographic origin of specimens is often helpful for species recognition; however, ITS sequences are frequently required for a reliable identification.

**Citation**: Magain N, Miadlikowska J, Goffinet B, et al. 2023. High species richness in the lichen genus Peltigera (Ascomycota, Lecanoromycetes): 34 species in the dolichorhizoid and scabrosoid clades of section Polydactylon, including 24 new to science. Persoonia 51: 1–88. https://doi.org/10.3767/persoonia.2023.51.01.
Effectively published online: 8 August 2023 [Received: 3 November 2021; Accepted: 10 October 2022].

## INTRODUCTION

Lichen-forming fungi of the genus *Peltigera* are amongst the earliest described (Linnaeus 1753, Willdenow 1787). The thalli they form are usually large and conspicuous and grow mostly on mosses or directly on various substrata (soil, rock outcrops, the base of trees and rarely also on the trunk or branches) in dry to humid grasslands and forest environments. Following the recent assessment by Cannon et al. (2021), the genus can be easily recognised by its foliose thallus, forming compact to

---

[1] Evolution and Conservation Biology, InBioS Research Center, University of Liège, Sart Tilman B22, Quartier vallée 1, Chemin de la vallée 4, B-4000 Liège, Belgium; corresponding author e-mail: nicolas.magain@uliege.be.
[2] Department of Biology, Duke University, Box 90338, Durham, North Carolina, 27708 USA.
[3] Ecology and Evolutionary Biology, Unit 3043, University of Connecticut, 75 North Eagleville road, Storrs CT, 06269-3043 USA.
[4] Beaty Biodiversity Museum, University of British Columbia, Vancouver, British Columbia, V6T 1Z4, Canada.
[5] Institute of Ecology and Earth Sciences, University of Tartu, J. Liivi 2, Tartu 50409, Estonia; Institute of Agricultural & Environmental Sciences, Estonian University of Life Sciences, Fr. R. Kreutzwaldi 5, Tartu 51006, Estonia
[6] Science & Education, The Field Museum, 1400 S. Lake Shore Drive, Chicago, Illinois, 60605 USA.
[7] Licenciatura en Biología, Universidad Distrital Francisco José de Caldas, Cra. 4 No. 26B-54, Torre de Laboratorios, Herbario, Bogotá, Colombia; current address: Botanischer Garten, Freie Universität Berlin, Königin-Luise-Straße 6–8, 14195 Berlin, Germany.
[8] Botanischer Garten, Freie Universität Berlin, Königin-Luise-Straße 6–8, 14195 Berlin, Germany.
[9] Laboratório de Botânica / Liquenologia, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande – MS, Brazil.
[10] Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, CAS, Kunming 650201, China.
[11] Natural and Behavioral Sciences Division, University of Maine – Fort Kent, Fort Kent, ME, USA.
[12] Division of Biological Sciences, University of Montana, Missoula, MT, USA.

wide-spreading rosettes, with lobes rounded or elongate, bright green, blue-grey, grey-brown or brown, flat, wavy or bullate, smooth, matt or shiny, scabrous, tomentose or pruinose, smooth or with folioles or soralia; a non-corticate lower surface, densely arachnoid-tomentose or with anastomosing, pale or dark veins, from which arise conspicuous rhizines; pseudoparenchymatous cortex; cephalodia sometimes present; ascomata apothecia, saddle-shaped, flattened or oval, red-brown to black, often reflexed and becoming ± curved and bean-shaped or with crenulate margins, on horizontal or vertical, ascending lobes; asci 8-spored, cylindrical, fissitunicate, the apex with a well-developed K/I+ blue ring, *Peltigera*-type; complex chemistry either present or not, including tenuiorin, methyl gyrophorate and gyrophoric acid and additional hopane triterpenoids.

The most morphologically similar genera are *Solorina*, which differs by its immersed apothecia, *Nephroma*, which forms apothecia on the underside, and *Yoshimuriella*, which forms a similar vein pattern on the underside but always has horizontal apothecia, lacks rhizines, and is generally epiphytic.

Although *Peltigera* is easily recognised at the genus level, species identification can be very difficult. Common cases of high intraspecific and low interspecific variation can result in a paucity of diagnostic phenotypic characters to separate species. Despite the taxonomic difficulties at the species level, the genus is widely used in ecosystem evaluations, including radioactive contamination (Nifontova 1996, Seaward 2002) and nature protection (Nordén et al. 2007), as well as in ecological assessments of global climate change (Darnajoux et al. 2015, Vallese et al. 2021) and biological nitrogen fixation (Hodkinson et al. 2014, Darnajoux et al. 2014, 2017, 2019). *Peltigera* has also been utilized as a model system in physiological, genomic and transcriptomic studies of the lichen symbiosis (Miao et al. 2012, Kampa et al. 2013, Grube et al. 2014, Díaz et al. 2015, Steinhäuser et al. 2016) and its mitochondrial genome was the first assembled amongst all lichenized fungi (Xavier et al. 2012). A recent study also addressed the composition of its microbiome (Leiva et al. 2021).

Increasingly, this genus has been the subject of multiple studies addressing mycobiont-photobiont symbiotic patterns of associations from local to global spatial scales, with contributions by O'Brien et al. (2013), Magain et al. (2017a, 2018), Chagnon et al. (2018, 2019), Lu et al. (2018), Pardo-De la Hoz et al. (2018) and Jüriado et al. (2019), resulting in its emergence as a model system for eco-evolutionary studies of symbiotic interactions.

Past taxonomic revisions of the genus were mostly restricted to specific geographic areas (Holtan-Hartwig 1993, Vitikainen 1994a, 1998, 2002, Goward et al. 1995, Galloway 2000, Louwhoff 2008, 2009). The existing estimate of the global number of species for the genus *Peltigera* (Lücking et al. 2017a) and their geographical distributions are largely based on morphologically circumscribed species (Martínez et al. 2003). The genus was among the first lichen-forming fungi to be subjected to a molecular phylogenetic revision (Miadlikowska & Lutzoni 2000, 2004) resulting in a strongly supported subgeneric classification into eight sections that was confirmed by multiple subsequent molecular studies (Miadlikowska et al. 2014, Magain et al. 2017a, 2018). More recently, all sections (except sections *Phlebia* and *Horizontales*) have been the subject of comprehensive molecular revisions, including photobiont identity and bidirectional (fungal and *Nostoc*) partner specialization at various spatial scales (Magain et al. 2017a, b, 2018, Miadlikowska et al. 2018, Pardo-De la Hoz et al. 2018). Early on (Goffinet & Miadlikowska 1999) and consistently, the recognition of new *Peltigera* species has been based on combinations of morphological, chemical and molecular characters (Goffinet et al. 2003, Miadlikowska et al. 2003, O'Brien et al. 2009, Sérusiaux et al. 2009, Lendemer & O'Brien 2011, Han et al. 2013, 2015, 2018, 2019, Miadlikowska et al. 2014, 2020, Magain et al. 2016, 2020, Manoharan-Basil et al. 2016).

Miadlikowska et al. (2003) pioneered the use of molecular barcodes for the taxonomy of lichen-forming fungi by selecting an 8–122 bp hypervariable motif within the internal transcribed spacer 1 sequence (ITS1-HR) for species recognition in section *Peltigera*. Subsequently, Magain et al. (2018) confirmed the suitability of the ITS1-HR to diagnose species in that section, based on an expanded taxon sampling and multiple species recognition and validation methods. The whole ITS region was proposed as an official barcode locus for the kingdom Fungi by Schoch et al. (2012) and has since then been widely used to identify species.

In the order *Peltigerales*, congruence among morphological, chemical and molecular data at the species level was demonstrated in the genus *Nephroma* (Sérusiaux et al. 2011). However, in several lichen groups, DNA-based species circumscriptions do not match species delimitations based on morphological and chemical traits and species cannot be reliably identified without DNA, e.g., in *Cladonia* (Pino-Bodas et al. 2013, 2015) and *Vulpicida* (Saag et al. 2014). Several times, the morphological characters that have been commonly used for species delimitation have been shown not to be valid within a molecular phylogenetic context, e.g., in the *Pectenia* complex (*Pannariaceae*) in Western Europe (Otálora et al. 2017) and the genus *Xanthoparmelia* (Leavitt et al. 2018). In other cases, the molecular signal is much more complex than the phenotypic make-up, as reported in the *Parmotrema reticulatum* group (*Lecanorales*; Del-Prado et al. 2016) and *Thamnolia vermicularis* (*Pertusariales*; Onuţ-Brännström et al. 2017). In some cases, refined concepts resulting from molecular revisions could be correlated to new or previously neglected morphological characters, including in several genera of *Peltigerales* such as *Coccocarpia* (Coca & Lücking 2016), *Lobariella* (Moncada et al. 2013b), *Pseudocyphellaria* (Miadlikowska et al. 2002, Moncada et al. 2014b, Lücking et al. 2017b) and *Sticta* (Moncada et al. 2014a, Magain & Sérusiaux 2015a, Simon et al. 2018).

Molecular species discovery and validation methods based on the species concept of 'separately evolving metapopulation lineages' (De Queiroz 2005, 2007) are commonly used for delimiting species, including lichen-forming fungi (e.g., Rannala 2015, Leavitt et al. 2016a, Boluda et al. 2019, Spjut et al. 2020). Based on a world-wide sampling and multilocus data for section *Polydactylon* of the genus *Peltigera*, Magain et al. (2017b) delimited species using species discovery (Structurama: Huelsenbeck et al. 2011, bGMYC: Reid & Carstens 2012, bPTP: Zhang et al. 2013) and validation methods (spedeSTEM: Ence & Carstens 2011, BPP: Yang & Rannala 2010), and proposed revised species delimitations based on a consensus of these methods.

This study is a follow-up on the results of Magain et al. (2017b) focusing on species from two of the three strongly-supported clades in section *Polydactylon*: the dolichorhizoid and the scabrosoid clades. We provide formal descriptions of all recognised species in these two clades, including morphological, chemical (secondary metabolites) and geographical (distribution ranges) circumscriptions, as well as the identity of their symbionts in terms of *Nostoc* phylogroups (Magain et al. 2017a, b). We further examined all species representing morphotypes of *Peltigera dolichorhiza*, *P. neopolydactyla*, *P. polydactylon*, *P. pulverulenta* and *P. scabrosa*. Although species of the polydactyloid clade are included in keys and figures, their detailed descriptions will be provided in a forthcoming paper, pending further studies with more material from Asia and Australasia. In the polydactyloid clade, two new taxa, closely related to *P. polydactylon* s.str. were recognised (Magain et al. 2016), and a new species was described from Papua New Guinea (Magain et al. 2020).

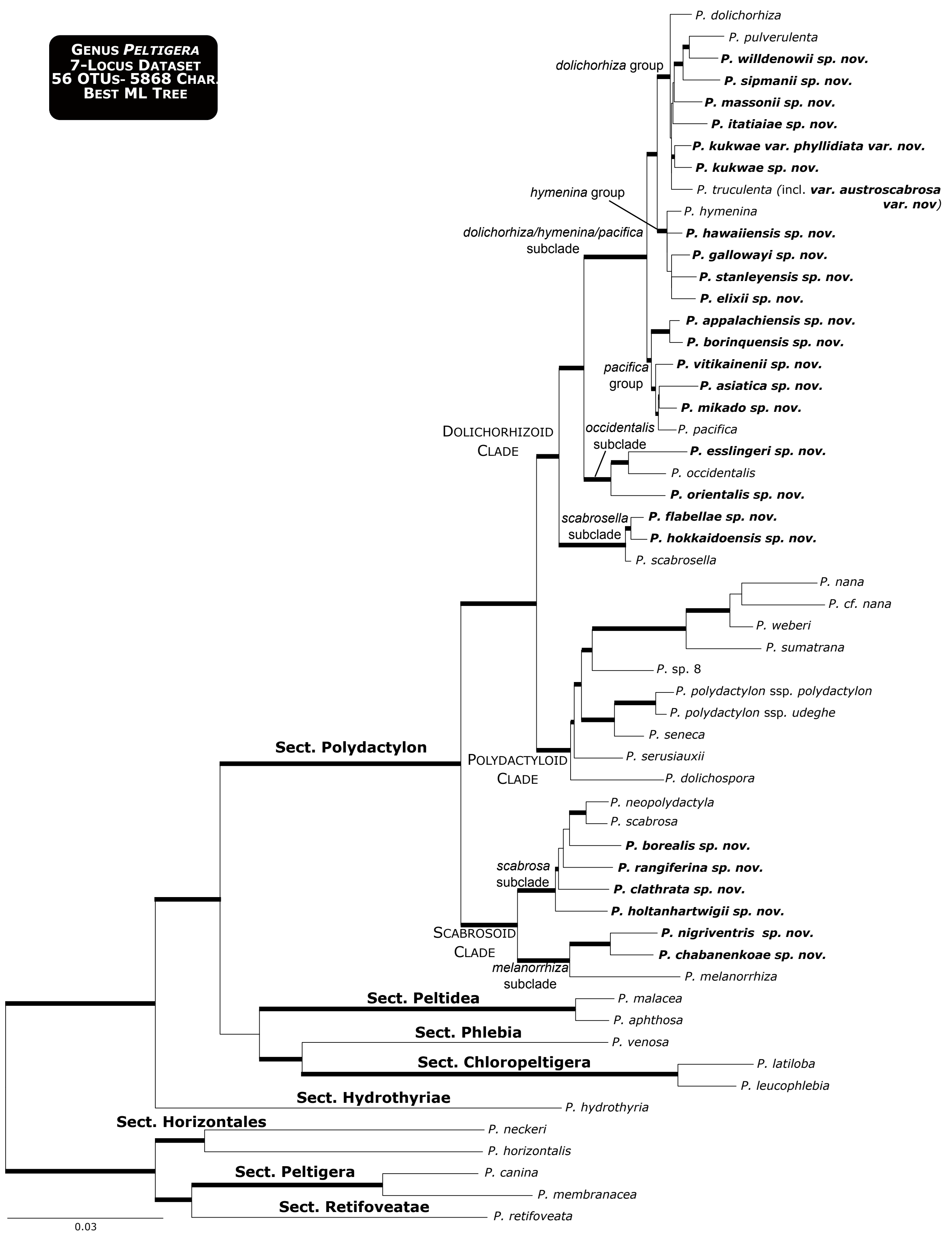

**Fig. 1** Phylogeny of the genus *Peltigera* highlighting the eight sections (**bold**) recognised in the genus (following Miadlikowska & Lutzoni 2000) with a focus on section *Polydactylon* and its three main clades (following Magain et al. 2017a). Best ML tree resulted from a RAxML analysis of the 7-locus (5868 characters) dataset for 56 OTUs. Within section *Polydactylon*, each terminal branch corresponds to a distinct evolutionary lineage as delimited by BPP analyses completed in this study for the scabrosoid and dolichorhizoid clades and following Magain et al. (2017a) for the polydactyloid clade. Taxa newly described in this study are shown in **bold**. Rooting of the tree follows a RAxML analysis including two *Solorina* species as outgroup (see Materials and Methods). Thick branches have bootstrap support values equal to or above 70 %.

## MATERIALS AND METHODS

### *Specimen examination*

This study is based on 375 specimens, integrating morphological, chemical and molecular characters together with field observations on habitat and geographical distribution when available. Specimens were collected during various field trips as well as borrowed from numerous fungaria (AMNH, ANDES, B, BG, BORH, BR, CANB, CBG, CDS, CGMS, CONC, CONN, DUKE, F, G, H, KOBL, LA, LE, LG, MA, MAF, MEXU, MHA, NSPM, NY, O, OMA, OSC, PERTH, PMAE, QFA, SAKH, TAIE, TUF, UBC, UDBC, UGDA, UPS and W) and personal fungaria.

All characters as evaluated by Cannon et al. (2021) have been examined, incl. thallus size, form, colour (incl. change of colour when wet or dry) and branching pattern; any character displayed by the upper surface, including shine and brightness, and any propagule produced; any character displayed by the rhizines development, size and shape; any character displayed by the ascomata.

Cannon et al. (2021) described ascospores as 'narrowly fusiform to acicular, usually 3-septate or occasionally multiseptate, colourless to pale brown'. Ascospores are rarely examined in taxonomical or phylogenetical studies on *Peltigera* and their traits are not included in identification keys (Holtan-Hartwig 1993, Vitikainen 2007, Cannon et al. 2021). We examined the ascospores of at least one representative collection of each recognised species with a Nikon Eclipse E-100 microscope. Mature apothecia were sectioned, and the hymenium was gently squashed in tap water with the addition of 1 % KOH solution in most cases to help detecting and releasing the mature ascospores from asci. The shape, septation and size are provided only for such examined ascospores.

Species identity of all specimens listed in 'selected specimens examined' sections later in the text have been confirmed with ITS sequences. Reference to *Nostoc* phylogroup(s) of all species are included following Magain et al. (2017a, b).

### *Chemistry*

Thin-layer-chromatography (TLC) was performed on representative specimens of all species studied, following Orange et al. (2010) and using solvents C and G. The purpose of TLC was to assess the presence or absence of the three main depsides (tenuiorin, methylgyrophorate, gyrophoric acid), and the three main triterpenes (dolichorrhizin, peltidactylin, zeorin) that can be helpful in species identification. Accessory substances were also annotated with numbers from 1–20. Matching with the accessory substances of Holtan-Hartwig (1993) and Vitikainen (1994a) proved to be difficult and was therefore abandoned: our numbering of these substances is therefore specific to this work. The observed concentration of each of the main depsides and triterpenes on the TLC plates was categorized as: major, minor or trace.

All recognised species within the dolichorhizioid and scabrosoid clades were tested at least on two collections, including the type for all new species or the epitype for those concerned by this nomenclatural procedure. Within each subclade or group (Fig. 1), tests were performed on several collections (not listed) to check for any variation regarding the main depsides and triterpenes. Specimens examined by TLC and the detected metabolites are also included in Suppl. Table S1 and S2.

### *Sequencing of ancient DNA from types*

DNA was extracted from the lectotype of *Peltigera scabrosa* (Greenland, Breutel, Flora Germaniae Exsiccati 203, UPS) and the holotype *of Peltigera polydactylon* var. *conjungens* (Australia, Queensland, Toowoomba, *C.H. Hartmann s.n.*, G! specimen G00053915) using the ClearYield$^{TM}$ kit from BioLink Laboratories (Washington, DC, USA) following the manufacturer's instructions. Genomic DNA was sent to the Duke Center for Genomic and Computational Biology (Durham, NC, USA) for library preparation and sequencing. Libraries were sequenced with an Illumina NovaSeq 6000 S Prime flow cell (2 × 150 bp). We trimmed low quality read ends (< Q20) using Trimmomatic v. 0.39 (Bolger et al. 2014) and assembled the metagenomes using the –meta option in Spades v. 3.14.1 (Bankevich et al. 2012) with kmers sizes 45, 65 and 85 bp. We then conducted a blastn search on the assembled metagenomic contigs using the 5.8S sequence of *Peltigera pulverulenta* GenBank OM349079. Finally, from each metagenome assembly, we extracted the subject contig that contained the blast hit to the 5.8S region and ran ITSx (Bengtsson-Palme et al. 2013) to delimit and assemble the ITS1, 5.8S and ITS2 regions. Similar attempts on types of *Peltigera dolichorhiza*, *P. neopolydactyla* and *P. pulverulenta* were unsuccessful.

### *Molecular data acquisition, phylogenetic analyses and species delimitation*

For the dolichorhizoid clade, we used the 94-specimen 8-locus (ITS, β-tubulin, *EFT2.1*, *RPB1*, LSU, COR1b, COR3 and COR16) dataset from Magain et al. (2017b), to which we added 31 sequences from six individuals, for a total of 100 representatives (Table 1). DNA extraction, locus amplification and sequencing follow Magain et al. (2017b). We also assembled a 7-locus dataset for the entire genus *Peltigera* (ITS, β-tubulin, *RPB1*, LSU, COR1b, COR3 and COR16) consisting of one representative per delimited species in section *Polydactylon*, as well as representatives of other sections of *Peltigera* (56 taxa) and two representatives of the sister genus *Solorina* (*Solorina crocea* and *S. saccata*), which were used to root the ingroup (58 *Peltigera* taxa and 5868 characters; Table 1), following Miadlikowska et al. (2014).

We ran PartitionFinder v. 2.1.1 (Lanfear et al. 2012, 2016) using the BIC criterion and the greedy algorithm. The dolichorhizoid 8-locus dataset was partitioned into 19 subsets: ITS1, ITS2, 5.8S, LSU, each of the three protein-coding genes (*EFT2.1*, *RPB1* and β-tubulin) partitioned according to codon positions and non-coding regions, COR1b, COR3 and COR16. The best scheme retrieved by PartitionFinder was composed of two subsets, the first one composed of β-tubulin 3rd codon position + non-coding regions + *RPB1* 3rd codon position + *EFT2.1* 3rd codon position + non-coding regions + ITS1 + ITS2 + COR1b + COR3 + COR16; the second one composed of LSU + 5.8S + β-tubulin 1st, 2nd codon positions + *EFT2.1* 1st, 2nd codon positions + *RPB1* 1st, 2nd codon positions + non-coding regions. For the analysis on the whole genus, we partitioned the dataset into 13 subsets: ITS, LSU, each codon position and non-coding regions for β-tubulin and RPB1, COR1b, COR3 and COR16. The best scheme was composed of three subsets: ITS; COR1b + COR3 + COR16 + β-tubulin and *RPB1* 3rd codon positions + non-coding regions of β-tubulin; LSU + β-tubulin 1st, 2nd codon positions + *RPB1* 1st, 2nd codon positions + *RPB1* non-coding regions.

We ran RaxML v. 8.2.10 (Stamatakis 2006, Stamatakis et al. 2008) as implemented on the CIPRES Science Gateway (Miller et al. 2010). Optimal tree and bootstrap searches were conducted with the rapid hill-climbing algorithm for 1000 replicates with GTR substitution model (Rodríguez et al. 1990) and gamma distribution parameter approximated with four categories, using the best scheme retrieved by PartitionFinder as a partition, on the two datasets (8-locus dataset for the dolichorhizoid clade and 7-locus dataset for the entire genus *Peltigera*).

We ran BPP v. 3.3 (Yang & Rannala 2010, 2014) using unguided species delimitation analysis (A11, estimating the species tree and the species delimitation at the same time). This analysis attempts to merge populations into one species and uses

**Table 1** Voucher information and GenBank accessions for specimens used in this study in phylogenetic analyses and type specimens. Newly generated sequences are shown in **bold**. Underlined specimens in the dolichorhizoid and scabrosoid clades were selected to represent species in the newly generated phylogeny of the genus (Fig. 1).

| Clade & taxon | DNA no. | Voucher | ITS | ß-tubulin | *RPB1* | *EFT*2.1 | LSU | COR1b | COR3 | COR16 |
|---|---|---|---|---|---|---|---|---|---|---|
| **Dolichorhizoid Clade** | | | | | | | | | | |
| *Peltigera appalachiensis* **holotype** | P654 | USA, North Carolina; *J. Miadlikowska et al.* 10.09.2011-P654; DUKE | **OM339151** | – | – | – | – | – | – | – |
| *P. appalachiensis* | P3060 | Canada, British Columbia; *C. Björk* 16545; UBC | MF908484 | MF946754 | MF946711 | MF946675 | MF946789 | MF947048 | MF946939 | MF946834 |
| | N1939 | USA, Alabama; *B. Goffinet* 5209; DUKE | KX897224 | KX880111 | KX880217 | KX897475 | KX869776 | MF947049 | MF946940 | MF946835 |
| | N1944 | USA, Alaska; *B. Goffinet* 9424; CONN | KX897219 | KX880107 | KX880213 | KX897472 | KX869772 | MF947050 | MF946941 | MF946836 |
| | P1252 | USA, Arkansas; *J. Hollinger* 1781; UBC | KX897227 | KX880114 | KX880220 | MF946676 | KX869779 | MF947052 | MF946942 | MF946837 |
| | P309 | Canada, Québec; *J. Miadlikowska et al.* 2011-P309; DUKE | KX897220 | KX880108 | KX880214 | KX897473 | KX869773 | MF947051 | MF946943 | MF946838 |
| | P411 | Russia, Yakutia; *T. Ahti* 65064; H | KX897221 | KX880109 | KX880215 | MF946677 | KX869774 | MF947053 | MF946944 | MF946839 |
| | P640 | USA, North Carolina; *J. Miadlikowska et al.* 2011-P640; DUKE | KX897225 | KX880112 | KX880218 | KX897476 | KX869777 | MF947054 | MF946945 | MF946840 |
| | P645 | USA, North Carolina; *J. Miadlikowska et al.* 2011-P645; DUKE | KX897226 | KX880113 | KX880219 | KX897477 | KX869778 | MF947055 | MF946946 | MF946841 |
| | P845 | Norway; *N. Magain* DNA-P845; LG | KX897223 | KX880110 | KX880216 | KX897474 | KX869775 | MF947056 | MF946947 | MF946842 |
| *P. asiatica* **holotype** | P859 | Vietnam; *Vo Thi Phi Giao* G06-NL86B; PHH | KX897247 | KX880124 | KX880228 | – | KX869788 | MF947064 | MF946959 | MF946854 |
| *P. borinquensis* | P325 | Peru; *E. Gaya* 07.14.10-19; DUKE | KX897228 | KX880115 | KX880221 | KX897478 | KX869780 | MF947057 | MF946948 | MF946843 |
| | P6133 | Panama; *N. Magain* NM113; DUKE | **MT488026** | **MT521412** | – | – | – | – | – | **MW889922** |
| *P. borinquensis* **holotype** | P2024 | Puerto Rico; *R. Harris* 27299; DUKE | **MT488027** | – | – | – | – | – | – | – |
| *P. dolichorhiza* **epitype** | P937 | Colombia; *B. Moncada & R. Lücking* 33660; UDBC C-0009731 | **OM321433** | – | – | – | – | – | – | – |
| *P. dolichorhiza* | N1942 | Panama; *B. Goffinet* 753; CONN | KX897184 | KX880095 | KX880195 | KX897459 | KX869753 | – | – | – |
| | N789 | Madagascar; *E. Sérusiaux* s.n.; LG | MF908481 | MF946748 | MF946706 | – | MF946785 | MF947033 | MF946923 | MF946820 |
| | N999 | Reunion Island; *N. Magain & E. Sérusiaux* s.n.; LG | KX897180 | KX880093 | KX880193 | KX897457 | KX869751 | MF947034 | MF946924 | MF946821 |
| | P1551 | Galapagos Islands; *F. Bungartz* 8368; CDS 41014 | MF908482 | MF946749 | MF946707 | MF946670 | MF946786 | MF947035 | MF946925 | MF946822 |
| | P1596 | Brazil, Minas Gerais; *J. Miadlikowska et al.*; CGMS 34453 | KX897187 | KX880096 | KX880196 | KX897460 | KX869754 | MF947036 | MF946926 | MF946824 |
| | P28 | Costa Rica; *J. Miadlikowska et al.* 03.23.2003-P28; DUKE | KX897181 | KX880094 | KX880194 | KX897458 | KX869752 | MF947037 | MF946927 | MF946823 |
| | P348 | Mexico; *M.A. Herrera-Campos* 13382; MEXU | KX897182 | KM005819 | KM005937 | KM005875 | KM005745 | MF947038 | MF946928 | MF946825 |
| | P879 | Rwanda; *E. Sérusiaux* PA7; LG | KX897183 | MF946750 | MF946708 | MF946671 | – | MF947039 | MF946929 | MF946824 |
| | P893 | Bolivia; *M. Kukwa* 9740; UGDA 17730 | KX897179 | KX880092 | KX880192 | KX897456 | KX869750 | MF947040 | MF946930 | MF946827 |
| | P1202 | Mexico; *M.A. Herrera-Campos* 2658; MEXU | MF908483 | MF946752 | MF946710 | MF946673 | MF946788 | MF947043 | MF946933 | MF946830 |
| *P. elixii* **holotype** | N1545 | Papua New Guinea; *E. Sérusiaux* DNA1545; UPNG | KX897354 | MF946769 | KX880274 | KX897521 | KX869836 | – | – | – |
| *P.* cf. *elixii* | P1914 | Philippines; *K. Kalb* 12662; DUKE | **MT488025** | – | – | – | – | – | – | – |
| *P. esslingeri* **holotype** | P1650 | Honduras; *B. Allen* 17790; TEFH | KX897357 | KX880169 | KX880275 | – | KX869837 | MF947091 | MF946990 | MF946885 |
| *P. esslingeri* | P1734 | Peru; *N. Magain* DNA-P1734; DUKE | KX897356 | MF946770 | MF946727 | – | MF946801 | MF947092 | MF946991 | – |
| | P936 | Colombia; *R. Lücking* 33659; UDBC | KX897359 | KX880170 | KX880276 | MF946689 | KX869838 | MF947093 | MF946992 | MF946884 |
| | P6139 | Panama; *N. Magain* NM49; DUKE | **MT488031** | **MT521411** | **MT521416** | **MT563091** | **–** | **MW889914** | **MW889918** | **MW889923** |
| *P. flabellae* **holotype** | N1666 | Canada, British Columbia; *T. Tønsber*g 20741; UBC | KX897364 | KX880171 | KX880277 | KX897522 | KX869839 | MF947094 | MF946993 | MF946886 |
| *P. flabellae* | N1674 | Canada, British Columbia; *T. Tønsberg* 20742; BG 34877 | KX897361 | MF946771 | MF946728 | – | – | MF947095 | MF946994 | MF946887 |
| | P3055 | Canada, British Columbia; *T. Goward* 06-1371; UBC | MF908494 | MF946772 | MF946729 | MF946690 | MF946802 | MF947096 | MF946995 | MF946888 |
| *P. gallowayi* | P1530 | New Zealand; *D. Blanchon* s.n.; DUKE | KX897351 | KX880166 | KX880271 | KX897519 | KX869833 | – | MF946987 | MF946883 |
| *P. gallowayi* **holotype** | P3020 | New Zealand; *L. Tibell* 10248; AK | **OM955146** | – | – | – | – | – | – | – |
| *P. gallowayi* | P604 | New Zealand; *F. Högnabba* 1538; H | KX897346 | KX880164 | KX880269 | KX897517 | KX869831 | – | MF946988 | MF946882 |
| | P605 | New Zealand; *S. Stenroos* 5815; H | KX897352 | KX880167 | KX880272 | KX897520 | KX869834 | – | MF946989 | MF946881 |
| | P607 | New Zealand; *S. Stenroos* 5820; H | KX897348 | KX880165 | KX880270 | KX897518 | KX869832 | – | – | – |
| | P1627 | Australia; *H. Streiman* 50190; CBG | **MT488023** | – | – | – | – | – | – | – |
| *P. hawaiiensis* **holotype** | P1236 | USA, Hawaii; *B. McCune* 22196; OSC | KX897190 | KX880098 | – | – | KX869756 | – | MF946934 | – |
| *P. hokkaidoensis* | P1660 | Japan, Hokkaido; *G. Thor* 25408; UPS 519475 | KX897365 | KX880172 | KX880278 | MF946691 | KX869840 | MF947098 | MF946996 | MF946889 |
| | P1672 | Japan, Hokkaido; *G. Thor* s.n.; UPS | KX897366 | MF946773 | MF946731 | – | MF953390 | MF947097 | – | MF946890 |
| *P. hokkaidoensis* **holotype** | P1674 | Japan, Hokkaido; *G. Thor* 25401; TNS | KX897367 | – | – | – | – | – | – | – |
| *P. hymenina* var. *hymenina* | N357 | Spain, Tenerife; *E. Sérusiaux* s.n.; LG | KX897192 | KX880100 | KX880199 | KX897463 | KX869758 | – | – | – |

**Table 1** (cont.)

| Clade & taxon | DNA no. | Voucher | ITS | ß-tubulin | *RPB1* | *EFT*2.1 | LSU | COR1b | COR3 | COR16 |
|---|---|---|---|---|---|---|---|---|---|---|
| *P. hymenina* var. *hymenina* | P1229 | USA, Oregon; *B. McCune* 30448; OSC | KX897205 | KX880103 | KX880203 | KX897467 | KX869762 | MF947044 | MF946935 | – |
| *P. hymenina* var. *dissecta* | P1799 | Portugal, Azores; *P. Divakar* 6915a; MAF | KX897207 | KX880104 | KX880204 | KX897468 | KX869763 | – | – | – |
| *P. hymenina* var. *dissecta* | P1903 | Portugal, Azores; *P. Divakar* 6916s; MAF | KX897208 | KX880105 | KX880205 | MF946674 | KX869764 | MF947045 | MF946936 | MF946832 |
| *P. hymenina* var. *hymenina* | P430 | Canada, Newfoundland; *J. Lendemer* 10397; H | KX897191 | KX880099 | KX880198 | KX897462 | KX869757 | MF947046 | MF946937 | MF946831 |
| *P. hymenina* var. *dissecta* | P516 | Portugal, Azores; *E. Sérusiaux* s.n.; LG | KX897196 | MF946753 | – | KX897464 | KX869759 | MF947047 | MF946938 | MF946833 |
| *P. hymenina* var. *hymenina* | P539 | Norway; *N. Magain* s.n.; LG | KX897198 | KX880101 | KX880201 | KX897465 | KX869760 | – | – | – |
| *P. hymenina* var. *hymenina* | P80 | Iceland; *T. Ahti* 69347; H | KX897200 | KX880102 | KX880202 | KX897466 | KX869761 | – | – | – |
| *P. hymenina* var. *hymenina* | P1718 | Spain; *I. Martinez et al.* 1175; MA-Lichen 12143 | **MT488028** | – | – | – | – | – | – | – |
| *P. itatiaiae* | P1557 | Brazil, Minas Gerais; *J. Miadlikowska et al.* P103; CGMS 34562 | KX897342 | KX880163 | KX880268 | KX897516 | KX869830 | MF947090 | MF946985 | MF946879 |
| *P. itatiaiae* **holotype** | P1561 | Brazil, Minas Gerais; *J. Miadlikowska et al.* P103; CGMS 34399 | KX897341 | MF946768 | MF946726 | MF946688 | MF946800 | MF947089 | MF946986 | MF946880 |
| P. *kukwae* var. *kukwae* **holotype** | P1567 | Brazil, Minas Gerais; *J. Miadlikowska et al.* P103; CGMS 34530 | KX897188 | KX880097 | KX880197 | KX897461 | KX86975 | MF947042 | MF946932 | MF946828 |
| *P. kukwae* var. *kukwae* | P1575 | Brazil, Minas Gerais; *J. Miadlikowska et al.* P103; CGMS 34456 | KX897189 | MF946751 | MF946709 | MF946672 | MF946787 | MF947041 | MF946931 | MF946829 |
|  | P1935 | Ecuador; *C. Truong* 3979; DUKE | **MT488024** | **MT521410** | – | **MT563090** | – | **MW889913** | **MW889917** | **MW889921** |
| *P. kukwae* var. *phyllidiata* **holotype** | P885 | Bolivia; *M. Kukwa* 9276; LPB | KX897335 | KX880158 | KX880264 | KX897513 | KX869825 | MF947084 | MF946980 | MF946874 |
| *P. kukwae* var. *phyllidiata* | P886 | Bolivia; *M. Kukwa* 9327; UGDA 17713 | KX897336 | KX880159 | KX880265 | KX897514 | KX869826 | – | – | – |
|  | P909 | Colombia; *R. Lücking* 33339; UDBC | KX897337 | KX880160 | MF946724 | – | KX869827 | MF947085 | MF946981 | MF946875 |
| *P. massonii* | P1555 | Brazil, Minas Gerais; *J. Miadlikowska et al.* P103; CGMS 34544 | KX897338 | KX880161 | KX880266 | KX897515 | KX869828 | MF947086 | MF946982 | MF946877 |
|  | P1570 | Brazil, Minas Gerais; *J. Miadlikowska et al.* P103; CGMS 34526 | KX897339 | MF946767 | MF946725 | MF946687 | MF946799 | MF947087 | MF946983 | MF946876 |
|  | P907 | Colombia; *R. Lücking* 33361; UDBC | KX897340 | KX880162 | KX880267 | – | KX869829 | MF947088 | MF946984 | MF946878 |
|  | P1608 | Brazil, Minas Gerais; *J. Miadlikowska et al.* P103; CGMS | **MT488029** | **MT52141** | **MT521417** | **MT563092** | – | **MW889912** | **MW889915** | **MW889919** |
| *P. massonii* **holotype** | L6187 | Ecuador; *D. Masson* EC003; LG | **MT488056** | – | – | – | – | – | – | – |
| *P. mikado* | P1667 | Japan, Kochi; *G. Thor* 21279; UPS 164500 | KX897244 | KX880121 | KX880226 | – | KX869785 | MF947062 | MF946953 | MF946848 |
|  | N1929 | China, Yunnan; *B. Goffinet* 10120; CONN | KX897234 | KX880116 | KX880222 | KX897479 | KX869781 | MF947063 | MF946954 | MF946849 |
|  | P1291 | China, Yunnan; *J. Miadlikowska* 2003-P1291; DUKE | KX897241 | KX880118 | – | – | – | – | MF946955 | MF946850 |
| *P. mikado* **holotype** | T266 | Taiwan; *B. Goffinet & E. Sérusiaux* T266; TAIE | **MT488051** | – | – | – | – | – | – | – |
| *P. mikado* | P3032 | Russia, Khabarovsk Territory; *F. Lutzoni & J. Miadlikowska* 06.29.2013-P3032; DUKE | MF908486 | MF946759 | MF946714 | MF946680 | MF946791 | – | MF946956 | MF946851 |
| *P. occidentalis* | P1638 | USA, NC; *R.C. Harris* 52559; NY | KX897275 | MF946761 | MF946716 | – | MF946793 | MF947065 | MF946960 | MF946855 |
|  | P299 | Canada, Québec; *F. Lutzoni et al.* s.n.; DUKE | KX897269 | KX880133 | KX880237 | KX897489 | KX869798 | MF947066 | MF946961 | MF946856 |
|  | P3034 | Russia, Khabarovsk Territory; *F. Lutzoni & J. Miadlikowska* 07.26.2013-P3034; DUKE | MF908489 | MF946758 | MF946717 | MF946684 | MF946794 | – | – | – |
|  | P510 | Norway; *N. Magain* s.n.; LG | KX897276 | – | KX880239 | KX897491 | KX869800 | MF947067 | MF946962 | MF946857 |
|  | P521 | Norway; *N. Magain* s.n.; LG | KX897277 | – | KX880240 | KX897492 | KX869801 | – | – | – |
|  | P543 | Norway; *N. Magain* s.n.; LG | KX897272 | KX880134 | KX880238 | KX897490 | KX869799 | – | – | – |
|  | P866 | USA, Alaska; *T. Ahti* 63231; H | KX897278 | KX880135 | KX880241 | KX897493 | KX869802 | MF947068 | MF946963 | MF946858 |
|  | P103 | Canada, Québec; *J. Miadlikowska & F. Lutzoni* DNA-P103; DUKE | **MG811761** | – | – | – | – | – | – | – |
|  | N2049 | Norway; *S. Rui & E. Timdal* 9145; O L51747 | **MT488030** | – | – | – | – | – | – | – |
| *P. orientalis* **holotype** | P3304 | Japan; *E. Sérusiaux* DNA3304; TNS | MF908496 | MF946774 | MF946730 | – | MF946803 | MF947099 | MF946997 | MF946891 |
| *P. pacifica* | P1243 | Canada, British Columbia; *T. Goward* 06-1522; UBC | KX897283 | KX880136 | KX880242 | KX897494 | KX869804 | MF947069 | MF946964 | MF946860 |
|  | P443 | Canada, British Columbia; *O. Vitikainen* 13080; H | KX897284 | KM005822 | KM005938 | – | KM005762 | – | MF946965 | MF946859 |
| *P. pulverulenta* **epitype** | P1937 | Ecuador; *C. Truong* 3945; QCNE | **OM349079** | – | – | – | – | – | – | – |
| *P. pulverulenta* | P890 | Bolivia; *M. Kukwa* 8536; UGDA 17702 | KX897290 | KX880137 | KX880244 | KX897497 | KX869805 | MF947070 | MF946967 | MF946861 |
|  | P897 | Mexico; *M.A. Herrera-Campos* 122; MEXU | KX897291 | MF946762 | MF946718 | – | – | MF947071 | MF946966 | – |
|  | P901 | Colombia; *R. Lücking* 33383; UDBC | KX897295 | KX880138 | KX880245 | – | KX869806 | MF947072 | MF946968 | MF946862 |
|  | P938 | Colombia; *R. Lücking* 33321; UDBC | KX897296 | KX880139 | KX880246 | – | KX869807 | – | – | – |
|  | P945 | Colombia; *R. Lücking* 33691; UDBC | KX897297 | KX880140 | KX880247 | KX897498 | KX869808 | – | – | – |
|  | P953 | Colombia; *R. Lücking* 33333; UDBC | MF908490 | MF946763 | MF946720 | MF946685 | MF946795 | – | – | MF946865 |
| *P. scabrosella* | P536 | Norway; *N. Magain* s.n.; LG | KX897332 | KX880157 | KX880263 | KX897512 | KX869824 | MF947077 | MF946974 | MF946868 |

**Table 1** (cont.)

| Clade & taxon | DNA no. | Voucher | ITS | ß-tubulin | *RPB1* | *EFT*2.1 | LSU | COR1b | COR3 | COR16 |
|---|---|---|---|---|---|---|---|---|---|---|
| *P. scabrosella* (cont.) | P619 | Norway; *N. Magain* s.n.; LG | KX897330 | MF946765 | MF946721 | – | MF946797 | MF947078 | MF946973 | MF946869 |
| *P. sipmanii* | P1522 | Colombia; *R. Lücking* 34033; UDBC | KX897300 | KX880144 | KX880250 | KX897501 | KX869811 | MF947075 | MF946969 | MF946866 |
| | P1525 | Colombia; *D. Fonseca & F. Martinez* 199; UDBC | MF908491 | MF946764 | MF946719 | MF946686 | MF946796 | MF947076 | MF946970 | MF946867 |
| *P. sipmanii* **holotype** | P1930 | Ecuador; *C. Truong* 3942; DUKE | **MT488050** | – | **MT521418** | – | – | – | **MW889916** | **MW889920** |
| *P. stanleyensis* **holotype** | N1534 | Papua New Guinea; *E. Sérusiaux* DNA1534; UPNG | KX897353 | KX880168 | KX880273 | – | KX869835 | – | – | – |
| *P. truculenta* | P1251 | Chile; *J. Hollinger* 1925; UBC | KX897398 | KX880184 | – | KX897533 | KX869853 | – | – | – |
| | P1750 | Kerguelen Islands; *R.L. Poulsen* 767; H | MF908492 | MF946766 | MF946722 | – | – | MF947079 | MF946978 | MF946870 |
| | P329 | Chile; *P. Nelson* 4362; CONC | KX897397 | – | KX880289 | KX897532 | KX869852 | – | – | – |
| | P330 | Chile; *T. Wheeler* 3826; CONC | KX897400 | KX880186 | KX880291 | KX897535 | KX869855 | MF947082 | MF946975 | MF946871 |
| | P332 | Chile; *T. Wheeler & P. Nelson* 89; CONC | KX897396 | KX880183 | KX880288 | – | KX869851 | MF947081 | MF946976 | MF946872 |
| | P335 | Chile; *T. Wheeler* 1093; CONC | KX897399 | KX880185 | KX880290 | KX897534 | KX869854 | MF947083 | MF946979 | MF946873 |
| *P. truculenta* var. *austroscabrosa* **holotype** | 5540 | Chile; *B. Goffinet* 10501; CONC | **OM778710** | – | – | – | – | – | – | – |
| *P. truculenta* var. *austroscabrosa* | P3109 | Chile; *B. Shaw* 18074; DUKE | **MT488052** | **MT521415** | **MT521419** | **MT563093** | – | – | – | – |
| | P3016 | Gough Island; *M. Gremmen* 99-348; H | MF908493 | MF946760 | MF946723 | – | MF946798 | MF947080 | MF946977 | – |
| *P. vitikainenii* | P1662 | Japan, Hokkaido; *A. Frisch* 10/Jp410; UPS 522008 | KX897243 | KX880120 | KX880225 | MF946678 | KX869784 | MF947058 | MF946949 | MF946844 |
| *P. vitikainenii* **holotype** | P384 | Norway; *N. Magain & E. Timdal* P384; O | KX897237 | KX880117 | KX880223 | KX897480 | KX869782 | MF947059 | MF946950 | MF946845 |
| *P. vitikainenii* | P390 | Norway; *N. Magain* s.n.; LG | KX897246 | KX880123 | KX880227 | KX897481 | KX869787 | MF947060 | MF946951 | MF946846 |
| | P3069 | Canada, British Columbia; *T. Goward* 06-329c; UBC | MF908485 | MF946755 | MF946712 | MF946679 | MF946790 | MF947061 | MF946952 | MF946847 |
| | P1659 | Japan, Hokkaido; *G. Thor* 25720; UPS 519479 | KX897242 | KX880119 | KX880224 | MF946681 | KX869783 | – | MF946957 | MF946852 |
| | P3001 | Russia, Khabarovsk Territory; *F. Lutzoni & J. Miadlikowska* 2013-P3001; DUKE | MF908487 | MF946757 | MF946713 | MF946683 | MF946792 | – | MF946958 | MF946853 |
| | P3009 | Russia, Sakhalin; *S. Chabanenko* 3082; SAKH | MF908488 | MF946756 | MF946715 | MF946682 | – | – | – | – |
| *P. willdenowii* **holotype** | P1521 | Colombia; *R. Lücking* 34028; UDBC | KX897298 | KX880141 | KX880248 | KX897499 | KX869809 | MF947074 | MF946972 | MF946864 |
| *P. willdenowii* | P900 | Colombia; *R. Lücking* 33367; UDBC | KX897299 | KX880142 | KX880249 | KX897500 | KX869810 | MF947073 | MF946971 | MF946863 |
| **Polydactyloid Clade** | | | | | | | | | | |
| *P. dolichospora* | N1899 | China, Yunnan; *B. Goffinet* 10014; CONN | KX897390 | – | KX880286 | KX897530 | KX869848 | – | – | – |
| | N1921 | China, Yunnan; *B. Goffinet* 10064; CONN | KX897386 | MF946782 | MF946739 | MF946696 | MF946810 | – | MF947007 | – |
| *P. nana* | P1281 | China, Yunnan; *J. Miadlikowska* 10.24.2002-P1281; DUKE | KX897212 | – | KX880208 | – | KX869767 | MF947101 | MF946998 | – |
| *P.* cf. *nana* | P609 | New Zealand; *S. Stenroos* 6037; H | KX897217 | – | KX880212 | KX897471 | KX869771 | – | – | MF946893 |
| *P. polydactylon* ssp. *polydactylon* | P385 | Norway; *N. Magain* s.n.; LG | KX365448 | KM005820 | KM005994 | KM005876 | KM005765 | KX365489 | KX373621 | KX373632 |
| *P. polydactylon* ssp. *udeghe* | P71 | USA, New Mexico; *J. Hollinger* 2462; DUKE | KX365444 | KX365464 | KX365459 | KX897496 | KX365452 | KX365486 | KX373618 | KX373628 |
| *P. polydactylon* ssp. *udeghe* (var. *conjungens* **holotype)** | NA | Australia, Queensland; *C.H. Hartmann* s.n.; G00053915 | **OM913601** | – | – | – | – | – | – | – |
| *P. seneca* | P450 | USA, Pennsylvania; *J. Lendemer* 16792; NY | KX365451 | – | KX365463 | KX897531 | KX365458 | KX365490 | KX373623 | KX373634 |
| *P. serusiauxii* | N1532 | Papua New Guinea; *E. Sérusiaux* s.n.; LG | KX897391 | KX880180 | KX880287 | – | KX869849 | – | – | – |
| *P.* sp. 8 | N1922 | China, Yunnan; *B. Goffinet* 10072; CONN | KX897375 | KX880175 | KX880281 | KX897525 | KX869843 | MF947100 | MF947003 | MF946896 |
| *P. sumatrana* | P884 | Papua New Guinea; *E. Sérusiaux* 16402; LG | KX897395 | KX880182 | – | – | – | – | – | – |
| *P. weberi* | s.n. | Papua New Guinea; *H. Sipman* 39314; B | FJ527281 | – | – | – | – | – | – | – |
| **Scabrosoid Clade** | | | | | | | | | | |
| *P. borealis* **holotype** | P311 | Canada, Québec; *J. Miadlikowska & F. Lutzoni* 08.07. 2011-SN6W3, P0311; QFA | KX897305 | – | – | – | – | – | – | – |
| *P. borealis* | P1210 | Norway; *N. Magain* s.n.; LG | KX897301 | KX880145 | KX880251 | – | KX869812 | – | – | – |
| | P1250 | Canada, Alberta; *J. Hollinger* 1066; UBC | KX897302 | KX880146 | KX880252 | KX897502 | KX869813 | – | MF947020 | MF946912 |
| | P1539 | Russia, Krasnoyarsk Territory; *F. Lutzoni & J. Miadlikowska* 06.2012-P1539; DUKE | KX897303 | – | MF946747 | MF946703 | MF946817 | – | MF947021 | MF946913 |
| | P550 | Norway; *N. Magain* s.n.; LG | KX897308 | KX880148 | KX880254 | KX897504 | KX869815 | – | MF947023 | MF946915 |

**Table 1** (cont.)

| Clade & taxon | DNA no. | Voucher | ITS | ß-tubulin | *RPB1* | *EFT*2.1 | LSU | COR1b | COR3 | COR16 |
|---|---|---|---|---|---|---|---|---|---|---|
| *P. borealis* (cont.) | P97 | Canada, Québec; *F. Lutzoni et al.* 2011-P97; DUKE | KX897307 | KX880147 | KX880253 | KX897503 | KX869814 | – | MF947022 | MF946914 |
| *P. chabanenkoae* **holotype** | P3010 | Russia, Sakhalin; *S. Chabanenko* 3072; SAKH-3072 | MF908504 | MF946783 | MF946745 | MF946702 | MF946816 | – | MF947019 | MF946910 |
| *P. clathrata* | P1228 | USA, Oregon; *B. McCune* 30018; OSC | KX897259 | KX880129 | KX880234 | KX897487 | KX869794 | – | MF947016 | MF946908 |
| *P. clathrata* **holotype** | P1232 | USA, Oregon; *B. McCune* 26873; OSC | KX897260 | KX880130 | – | – | KX869795 | – | – | – |
| *P. clathrata* | P1257 | USA, Oregon; *J. Hollinger* 1385; UBC | KX897261 | KX880131 | KX880235 | KX897488 | KX869796 | – | – | – |
| *P. holtanhartwigii* | N1236 | Greenland; *E. Sérusiaux* DNA1236; LG | KX897320 | KX880153 | KX880259 | KX897509 | KX869820 | – | MF947029 | MF946922 |
|  | P865 | Russia, Yakutia; *T. Ahti* 65068; H | KX897319 | KX880152 | KX880258 | KX897508 | KX869819 | – | MF947030 | MF946920 |
| *P. holtanhartwigii* **holotype** | P1538 | Russia, Krasnoyarsk Territory; *J. Miadlikowska et al.* 24.06.2012-L10.3; LE | KX897322 | – | MF952737 | MF946705 | MF946819 | – | MF947028 | MF946921 |
| *P. melanorrhiza* | P1798 | Portugal, Azores; *P. Divakar* 6918b; MAF | KX897211 | KX880106 | KX880207 | KX897470 | KX869766 | – | MF947010 | MF946902 |
|  | P515 | Portugal, Azores; *E. Sérusiaux* s.n.; LG | KX897210 | – | KX880206 | KX897469 | KX869765 | – | – | – |
| *P. neopolydactyla* | P1212 | Norway; *N. Magain* s.n.; LG | KX897256 | – | KX880232 | KX897485 | KX869792 | – | – | – |
|  | P1537 | Russia, Krasnoyarsk Territory; *F. Lutzoni & J. Miadlikowska* 06.2012-P1537; DUKE | MF908500 | – | MF946740 | MF946698 | MF946811 | – | MF947011 | MF946903 |
|  | P1668 | Japan, Hokkaido; *G. Thor* 24306; UPS 519471 | KX897250 | KX880125 | KX880229 | KX897482 | KX869789 | – | MF947012 | MF946904 |
|  | P302 | Canada, Québec; *F. Lutzoni et al.* 2011-P302; DUKE | KX897252 | KX880126 | KX880230 | KX897483 | KX869790 | – | MF947013 | MF946905 |
|  | P3024 | Canada, Québec; *R. Darnajoux* P3024; DUKE | MF908501 | – | MF946741 | MF946699 | MF946812 | – | – | – |
|  | P3027 | Canada, Québec; *R. Darnajoux* P3027; DUKE | MF908502 | – | MF946742 | MF946700 | MF946813 | – | MF947014 | MF946906 |
|  | P321 | Canada, Québec; *F. Lutzoni et al.* 2011-P321; DUKE | KX897253 | KX880127 | KX880231 | KX897484 | KX869791 | – | – | – |
|  | P506 | Norway; *N. Magain* s.n.; LG | KX897257 | KX880128 | KX880233 | KX897486 | KX869793 | – | MF947015 | MF946907 |
|  | P669 | Norway; *N. Magain* s.n.; LG | KX897258 | – | MF946743 | MF946701 | – | – | – | – |
|  | P811 | Norway; *N. Magain* s.n.; LG | KX897255 | – | MF946744 | – | MF946814 | – | – | – |
| *P. nigriventris* **holotype** | P1231 | USA, Oregon; *B. McCune* 24160; OSC | KX897264 | KX880132 | KX880236 | – | KX869797 | – | MF947017 | MF946909 |
| *P. nigriventris* | P3051 | USA, Oregon; *J. Hollinger* 1386; UBC | MF908503 | – | – | – | MF946815 | – | MF947018 | MF946911 |
| *P. rangiferina* | P312 | Canada, Québec; *J. Miadlikowska et al.* SN6-E1; DUKE | KX897323 | KX880154 | KX880260 | KX897510 | KX869821 | – | MF947031 | – |
|  | P315 | Canada, Québec; *J. Miadlikowska et al.* SN9-C1-2; DUKE | KX897324 | KX880155 | KX880261 | – | KX869822 | – | – | – |
|  | P549 | Norway; *N. Magain* P549; LG | KX897327 | KX880156 | KX880262 | KX897511 | KX869823 | – | MF947032 | – |
| *P. rangiferina* **holotype** | P6042 | USA, Alaska; *R. Rosentreter* 18621; OSC | **MT659359** | – | – | – | – | – | – | – |
| *P. scabrosa* | P107 | Canada, Québec; *F. Lutzoni et al.* 2011-P107; DUKE | KX897310 | KM005791 | KM005933 | KM005872 | KM005769 | – | MF947024 | MF946916 |
| *P. scabrosa* **lectotype** | NA | Greenland; Breutel; *Flora Germaniae Exsiccati* 203; UPS | **OM913602** | – | – | – | – | – | – | – |
| *P. scabrosa* | P113 | Canada, Québec; *F. Lutzoni et al.* 2011-P113; DUKE | KX897311 | KX880149 | KX880255 | KX897505 | KX869816 | – | – | – |
|  | P1209 | Norway; *N. Magain* s.n.; LG | KX897312 | KX880150 | KX880256 | KX897506 | KX869817 | – | MF947025 | MF946917 |
|  | P1255 | Canada, British Columbia; *C. Björk* 16230; UBC | KX897313 | KX880151 | KX880257 | KX897507 | KX869818 | – | MF947026 | MF946918 |
|  | P1540 | Russia, Krasnoyarsk Territory; *F. Lutzoni & J. Miadlikowska* 06.24.2012-P1540; DUKE | KX897314 | – | MF946746 | – | MF946818 | – | MF947027 | MF946919 |
|  | P830 | Norway; *N. Magain* s.n.; LG | KX897318 | MF946784 | – | MF946704 | – | – | – | – |
| **Other sections and outgroup** |  |  |  |  |  |  |  |  |  |  |
| *P. aphthosa* | P788 | Norway; *N. Magain* s.n.; LG. | MK680346 | KM005826 | KM005941 | N/A | MK517881 | MK688642 | MK688750 | – |
| *P. canina* | P0014 | Iceland; *J. Miadlikowska & F. Lutzoni* s.n.; DUKE | KU954063 | KM005803 | KM005925 | N/A | KM005741 | MH770203 | MH770461 | MH769957 |
| *P. horizontalis* | P1274 | China, Jilin; *M. Sohrabi* 16639; MS Herb. | **MT488053** | KM005795 | KM005946 | N/A | KM005749 | – | MK519351 | MK519364 |
| *P. hydrothyria* | P1845 | Canada, Nova Scotia; *Anderson* 159031; NSPM | KM005789 | KM005811 | KM005985 | N/A | KM005752 | – | MK519352 | – |
| *P. latiloba* | P6080 | Canada, Nunavut; *C. Björk* s.n.; UBC | MH734668 | MH756856 | – | N/A | – | MH756888 | MH756990 | MH756923 |
| *P. leucophlebia* | P6062 | Iceland, Arnessysla; *J. Miadlikowska & F. Lutzoni* s.n.; DUKE | MH734705 | MH756850 | MH756781 | N/A | – | MH756897 | MH756933 | MH756912 |
| *P. malacea* | P1028 | Norway; *N. Magain* s.n.; LG. | MK680440 | KM005790 | KM005942 | N/A | KM005757 | MK688702 | MK688779 | – |
| *P. membranacea* | P0003 | Iceland; *Miadlikowska et al.* s.n.; DUKE | MH758426 | KM005814 | KM005923 | N/A | KM005758 | MH770161 | MH770421 | MH769915 |
| *P. neckeri* | P190 | Spain, Mallorca; *Crespo et al.* 6107B; MAF | MT488054 | MT521414 | MT521420 | N/A | MK517879 | MK519350 | MK519361 | – |
| *P. retifoveata* | P0074 | Russia, Sakha Republic; *T. Ahti* 61821; H | MH758213 | – | KM005931 | N/A | KM005767 | MH770010 | MH770257 | MH769757 |
| *P. venosa* | P1905 | Norway; *N. Magain* s.n.; LG. | **MT488055** | – | KM005962 | N/A | KM005772 | – | – | **MW889924** |
| *Solorina saccata* | sn | Russia, Karelia; *Ahti* (with *Fadayeva*) s.n.; PAH (PTZ) | – | – | KM005963 | N/A | KX869863 | – | – | – |
| *Solorina crocea* | sn | Russia, Karelia; *Ahti* (with *Fadayeva*) s.n.; PAH (PTZ) | – | – | DQ973066 | N/A | DQ973043 | – | – | – |

**Fig. 2** Phylogenetic relationships within the dolichorhizoid clade. Best ML tree resulted from the RAxML analysis on the 8-locus dataset (6 596 characters) for 100 OTUs. Rooting follows Fig. 1. Thick branches have a bootstrap support values equal to or above 70 %. Vertical bars indicate delimitations of species as circumscribed in this study. Species newly described are indicated in **bold**. Informal taxon names used in previous studies (Magain et al. 2017a, b) are indicated within parentheses.

several algorithms to change the species tree topology under a multispecies coalescent model. We ran the analysis on the dolichorhizoid and the scabrosoid clades separately, using the same dataset as for phylogenetic analyses for the dolichorhizoid clade, and the 35-specimen 7-locus dataset from Magain et al. (2017b) for the scabrosoid clade. We ran the analysis for 100 000 generations, sampling every generation and discarding 8 000 generations as burn-in. We tested different ranges of priors. For the dolichorhizoid clade, we tested a τ prior value of 0.03 and θ prior values of 0.005, 0.01, 0.015, 0.02 and 0.03. For the scabrosoid clade, we tested a τ prior value of 0.04 and θ prior value of 0.015, to directly compare the results to those of Magain et al. (2017b), as well as a τ prior value of 0.03 with θ prior values of 0.005, 0.01 and 0.015.

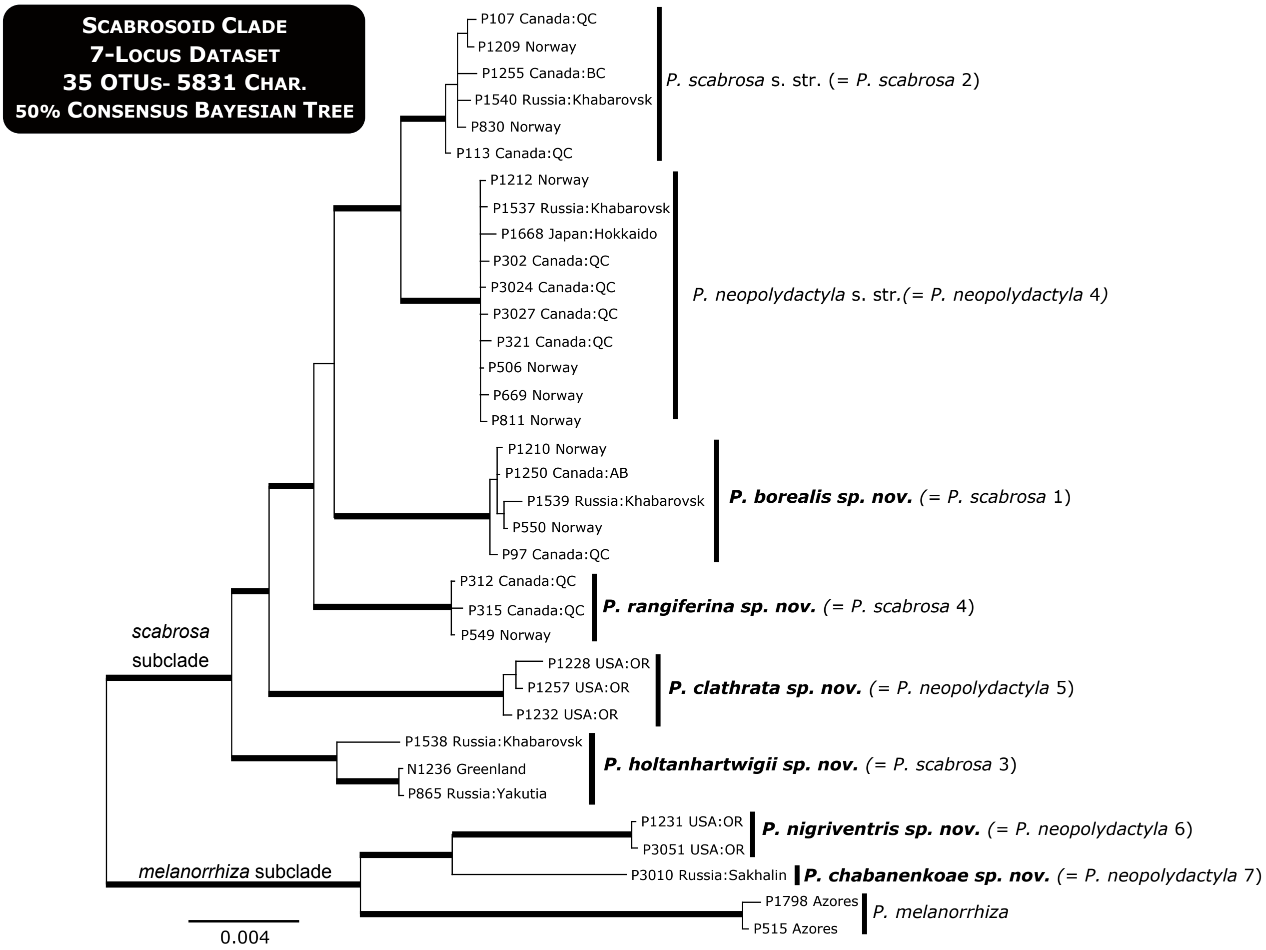

**Fig. 3** Phylogenetic relationships within the scabrosoid clade. 5 0% consensus Bayesian tree modified from Magain et al. (2017b). Thick branches have bootstrap support values equal to or above 70 %. Vertical bars indicate delimitations of species as circumscribed in this study. Species newly described are shown in **bold**. Informal taxon names used in previous studies (Magain et al. 2017a, b) are indicated in parentheses.

A priori assignment of species followed Magain et al. (2017b), and for the six additional specimens, we followed the results of the phylogenetic analyses: P1608 was assigned to *P. massonii* (sp. 2aa), P3109 to *P. truculenta*, P6133 to *P. borinquensis* (*neopolydactyla* 1b), P6139 to *P. esslingeri* (sp. 6). P1930 clustered close to *P. sipmanii* (*pulverulenta* 3) and was provisionally assigned to a new taxon *P. pulverulenta* 4 prior to BPP analyses, whereas P1935 clustered close to *P. kukwae* (former sp. 1 and former *dolichorhiza* 2) and was provisionally assigned to a new taxon *P. dolichorhiza* 3 (Table 1; Fig. 2). We tested 30 lineages in the dolichorhizoid clade corresponding to the species delimited in Fig. 2, with the additional splits of: *P. sipmanii* into two lineages (former *P. pulverulenta* 3 consisting of P1522 and P1525, and former *P. pulverulenta* 4 consisting of P1930); *P. massonii* into two lineages (former *P.* sp. 2aa consisting of P1555, P1570 and P1608 and former *P.* sp. 2ab consisting of P907); and P1202 and P1596 separated from *P. dolichorhiza* (as *P. dolichorhiza* b). We used the topologies that resulted from the ML analyses as guide trees for the analyses.

Magain et al. (2017b) suggested that *P. vitikainenii*, newly described in this paper, could be further split into two species (former *P. neopolydactyla* 2a: P384, P390, P1662, P3069 and former *P. neopolydactyla* 2c: P1659, P3001, P3009). However, we did not test the validity of these lineages, because they cannot be distinguished by the ITS, and *P. neopolydactyla* 2a does not appear monophyletic in our phylogeny (Fig. 2). In the scabrosoid clade, we tested 10 lineages, corresponding to the delimitation of species in Fig. 3, with the further delimitation of the former *P. scabrosa* 3a (N1236 and P865) and *P. scabrosa* 3b (P1538) following Magain et al. (2017b).

### *Barcodes for species*

For each recognised taxon, we provide a reference sequence (RefS) following the UNITE database definition (Kõljalg et al. 2013). The RefS is given by its corresponding GenBank accession number and is based on the type collection or on a collection best representing the population shown to be phylogenetically the most closely related to the type lineage. In addition, we examined the ITS1 and ITS2 regions for the presence of short unique motifs, which could serve as unequivocal identifiers for all recognised *Peltigera* species. For each newly described species, we provide one or several short barcodes composed of a few (1–18) nucleotides from the ITS sequence that allow unambiguous identification of the species. Each barcode is self-sufficient to recognise species, even when several barcodes are provided for a species.

## RESULTS AND DISCUSSION

### *Phylogeny and species delimitation*

The phylogeny of the genus *Peltigera* was first outlined by Miadlikowska & Lutzoni (2000), further elaborated by Miadlikowska et al. (2014) and most recently confirmed by Chagnon et al. (2019). Our analysis on the entire genus dataset confirmed the split of the genus in two major clades: one clade containing three sections: *Horizontales* and closely related *Peltigera* and *Retifoveatae*, and the second clade with section *Polydactylon*, sister to a clade composed of tri-partite sections: *Chloropeltigera*, *Phlebia* and *Peltidea* (Fig. 1) following the split (strongly supported for the first time) of section *Hydrothyria*e. Phylogenetic relationships within section *Polydactylon* are consistent with the topology from Magain et al. (2017b), showing three main well-supported clades: the dolichorhizoid clade (incl. *P. dolichorhiza* s.str., *P. hymenina* and *P. pulverulenta*), the polydactyloid clade (incl. *P. polydactylon*) and the scabrosoid clade (incl. *P. scabrosa* s.str. and *P. neopolydactyla* s.str.) (Fig. 1).

The results of BPP v. 3.3 analyses performed on the dolichorhizoid and scabrosoid clades are mostly congruent with species delimitation and validation presented in Magain et al. (2017b). In the dolichorhizoid clade (Fig. 2), *P. pulverulenta* 3 (P1522 and P1525 from Colombia) and *P. pulverulenta* 4 (P1930 from Ecuador) were merged into a single lineage corresponding to *P. sipmanii*, which is formally introduced below. *Peltigera dolichorhiza* 3, which represents a new lineage, clustered with *P.* sp. 1 and *P. dolichorhiza* 2 in the dolichorhizoid clade. Delimitation of some species varied depending on the priors tested, e.g., *P. scabrosella*, *P. hokkaidoensis* and *P. flabellae* were alternatively recovered as separate or a single species; the same was true for *P.* sp. 1, *P. dolichorhiza* 2 and *P. dolichorhiza* 3 (see below in Species inventory). In the first case, given their obvious morphological and geographical differences, we decided to consider *P. scabrosella*, *P. hokkaidoensis* and *P. flabellae* as three distinct species. Following this consensus approach, the dolichorhizoid clade consists of 25 species (Fig. 1, 2).

In the scabrosoid clade (Fig. 3), eight species were consistently delimited with $p > 0.95$ regardless of the priors we tested. However, *P. scabrosa* 3a and *P. scabrosa* 3b (Magain et al. 2017b) were merged together into a single lineage or sometimes considered as different lineages depending on the priors tested. Because of limited sampling of both putative species (two specimens for *P. scabrosa* 3a and one for *P. scabrosa* 3b), we included all three specimens within *P. holtanhartwigii* until future study validates their distinctiveness. Following this consensus approach, the scabrosoid clade consists of nine species (Fig. 1, 3).

### *Species inventory*

The dolichorhizoid clade includes 25 species: seven currently recognised species, and 18 species described as new to science below. These 25 species are part of three strongly supported subclades (Fig. 2):

- the *dolichorhiza/hymenina/pacifica* subclade (which does not include *P. neopolydactyla* s.str.) contains three strongly supported groups:
  - the *pacifica* group, which includes *P. pacifica* and five newly described species: *P. appalachiensis*, *P. asiatica*, *P. borinquensis*, *P. mikado* and *P. vitikainenii*;
  - the *dolichorhiza* group, which includes three already described species: *P. dolichorhiza*, *P. pulverulenta* and *P. truculenta*; and five newly described species: *P. itatiaiae*, *P. kukwae*, *P. massonii*, *P. sipmanii* and *P. willdenowii*, and two new varieties: *P. kukwae* var. *phyllidiata* and *P. truculenta* var. *austroscabrosa*;
  - the *hymenina* group, which includes *P. hymenina*, and four newly described species: *P. elixii*, *P. gallowayi*, *P. hawaiiensis* and *P. stanleyensis*; additionally, *P. dissecta*, which represents corticolous populations of *P. hymenina* in the Azores archipelago is proposed to be recognised as var. *dissecta*;
- the *occidentalis* subclade, which includes *P. occidentalis* and two newly described species: *P. esslingeri* and *P. orientalis*;
- the *scabrosella* subclade includes *P. scabrosella* and two newly described species: *P. flabellae* and *P. hokkaidoensis*.

The scabrosoid clade includes nine species, of which three are currently recognised and six are described as new to science below. These nine species are part of two strongly supported subclades:

- the *scabrosa* subclade, which includes two already described species: *P. neopolydactyla* and *P. scabrosa*; and four newly described species: three cryptic species with a scabrous upper thallus surface: *P. borealis*, *P. holtanhartwigii* and *P. rangiferina*; and *P. clathrata*, which lacks scabrosity on its upper thallus surface;
- the *melanorrhiza* subclade includes *P. melanorrhiza* and two newly described species: *P. chabanenkoae* and *P. nigriventris*.

Five additional putative new species recognised by Magain et al. (2017b) and another one (new lineage included in this study but not included in Table 2) are not formally described for the following reasons:

- *Peltigera* sp. 1, *P. dolichorhiza* 2 (P1567 and P1575) and *P. dolichorhiza* 3 (P1935) were considered as distinct lineages in most analyses. However, because of the limited number of representatives for *P. dolichorhiza* 2 and 3, obtained from a single locality each, and because some statistical tests suggested that the three lineages form a single species, we introduced *P. kukwae* to accommodate all three lineages. The monophyletic clade containing phyllidiate specimens of *P.* sp. 1 is recognised at the infraspecific level as *P. kukwae* var. *phyllidiata*.
- *Peltigera dolichorhiza* b (P1202 and P1596) was considered a single distinct species in most analyses, or sometimes split into two separate species (Magain et al. 2017b). However, because of insufficient material, it is tentatively included within *P. dolichorhiza*.
- *Peltigera* sp. 2ab (P907) discussed in Magain et al. (2017b) is included in *P. massonii*, because of a lack of strong statistical support to distinguish it from *P.* sp. 2a, and insufficient material (a single specimen);
- statistical delimitations distinguished two species within *P. vitikainenii* (*P. neopolydactyla* 2a and 2c). However, we propose to recognise a single species for the following reasons: a) both have identical ITS barcodes; b) both are morphologically or chemically indistinguishable; c) both share the same *Nostoc* phylogroups; and d) *P. neopolydactyla* 2a is not monophyletic. However, based on current data, both putative species have distinct distribution patterns: *P. neopolydactyla* 2c is restricted to East Asia whereas *P. neopolydactyla* 2a also occurs in North America and Europe where it is locally common. In the study by Magain et al. (2017b), COR1b and COR3 sequences provided evidence for the differentiation of two species, but it is also possible that *P. neopolydactyla* 2c represents a genetically divergent population within *P. vitikainenii* in Eastern Asia.
- *Peltigera scabrosa* 3a and 3b are merged into a single new species (*P. holtanhartwigii*) because representatives from both lineages are very rare and poorly sampled; further collections may justify the recognition of two species.

The potential species introduced as *Peltigera dolichorhiza* s.lat. A in Sérusiaux et al. (2009) from Papua New Guinea is not formally described in this study because it is represented by ITS sequences only. However, it is very likely to represent an additional new species in the *hymenina* group of the dolichorhizoid clade. Two collections by K. Kalb from the Philippines (from Luzon Island) were placed in the *hymenina* group and their ITS sequences differ from the newly described *P. elixii* by only a few nucleotide substitutions. However, their chemistry is very different from *P. elixii* because the four unknown terpenoids, which are autapomorphic for this widespread species in Papua New Guinea, were not detected. It is very likely that these specimens from the Philippines represent another undescribed species in the *hymenina* group. *Peltigera lyngei*,

**Table 2** Geographic ranges of species of *Peltigera* section *Polydactylon* within the main biogeographic regions detected in our study, as well as in the eight biogeographical realms of Olson et al. (2001). Numbers in parentheses represent the number of species endemic to that region. Total numbers include species but not infraspecific taxa.

| | North America (except Northwestern) | Northwestern North America | Hawaii | South and Central America | Antarctica | Africa, incl. Madagascar and Reunion | Europe and Macaronesia | North-East Asia (incl. Japan) | Yunnan, Taiwan and Indochina | Papua New Guinea | Australia and New Zealand |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Species of the **dolichorhizoid** clade | | | | | | | | | | | |
| Species name | | | | | | | | | | | |
| *P. dolichorhiza* | – | – | – | X | – | X | – | – | – | – | – |
| *P. itatiaiae* (*sp. nov.*) | – | – | – | X | – | – | – | – | – | – | – |
| *P. kukwae* var. *kukwae* (*sp. nov.*) | – | – | – | X | – | – | – | – | – | – | – |
| *P. kukwae* var. *phyllidiata* (*var. nov.*) | – | – | – | X | – | – | – | – | – | – | – |
| *P. massonii* (*sp. nov.*) | – | – | – | X | – | – | – | – | – | – | – |
| *P. pulverulenta* | – | – | – | X | – | – | – | – | – | – | – |
| *P. sipmanii* (*sp. nov.*) | – | – | – | X | – | – | – | – | – | – | – |
| *P. truculenta* | – | – | – | X | X | – | – | – | – | – | – |
| *P. truculenta* var. *austrosabrosa* (*var. nov.*) | – | – | – | X | X | – | – | – | – | – | – |
| *P. willdenowii* (*sp. nov.*) | – | – | – | X | – | – | – | – | – | – | – |
| *P. elixii* (*sp. nov.*) | – | – | – | – | – | – | – | – | – | X | – |
| *P. gallowayi* (*sp. nov.*) | – | – | – | – | – | – | – | – | – | – | X |
| *P. hawaiiensis* (*sp. nov.*) | – | – | X | – | – | – | – | – | – | – | – |
| *P. hymenina* var. *hymenina* | X | X | – | – | – | – | X | – | – | – | – |
| *P. hymenina* var. *dissecta* | – | – | – | – | – | – | X | – | – | – | – |
| *P. stanleyensis* (*sp. nov.*) | – | – | – | – | – | – | – | – | – | X | – |
| *P. appalachiensis* (*sp. nov.*) | X | – | – | – | – | – | X | X | – | – | – |
| *P. asiatica* (*sp. nov.*) | – | – | – | – | – | – | – | – | X | – | – |
| *P. borinquensis* (*sp. nov.*) | – | – | – | X | – | – | – | – | – | – | – |
| *P. mikado* (*sp. nov.*) | – | – | – | – | – | – | – | X | X | – | – |
| *P. pacifica* | – | X | – | – | – | – | – | – | – | – | – |
| *P. vitikainenii* (*sp. nov.*) | X | X | – | – | – | – | X | X | – | – | – |
| *P. esslingeri* (*sp. nov.*) | – | – | – | X | – | – | – | – | – | – | – |
| *P. occidentalis* | X | X | – | – | – | – | X | X | – | – | – |
| *P. orientalis* (*sp. nov.*) | – | – | – | – | – | – | – | X | – | – | – |
| *P. flabellae* (*sp. nov.*) | – | X | – | – | – | – | – | – | – | – | – |
| *P. hokkaidoensis* (*sp. nov.*) | – | – | – | – | – | – | – | X | – | – | – |
| *P. scabrosella* | X | ? | – | – | – | – | X | – | – | – | – |
| Total 26 (18 *sp. nov.*) | 4(0) | 5(2) | 1(1) | 10(8) | 1 | 1 | 5(0) | 6(2) | 2(1) | 2(2) | 1(1) |
| Biogeographical realms | Nearctic | | Oceania | Neotropics | Antarctica | Afrotropic | Palearctic | | Indo-Malay | | Australasia |
| Total 26 (Endemics) | 7 (2) | | 1(1) | 10 (8) | 1 | 1 | 9(2) | | 2(1) | | 3(3) |
| Species of the **scabrosoid** clade | | | | | | | | | | | |
| Species name | | | | | | | | | | | |
| *P. chabanenkoae* (*sp. nov.*) | – | – | – | – | – | – | – | X | – | – | – |
| *P. melanorrhiza* | – | – | – | – | – | – | X | – | – | – | – |
| *P. nigriventris* (*sp. nov.*) | – | X | – | – | – | – | – | – | – | – | – |
| *P. clathrata* (*sp. nov.*) | – | X | – | – | – | – | – | – | – | – | – |
| *P. borealis* (*sp. nov.*) | X | – | – | – | – | – | X | X | – | – | – |
| *P. holtanhartwigii* (*sp. nov.*) | X | – | – | – | – | – | – | X | – | – | – |
| *P. neopolydactyla* | X | X | – | – | – | – | X | X | – | – | – |
| *P. rangiferina* (*sp. nov.*) | X | – | – | – | – | – | X | – | – | – | – |
| *P. scabrosa* | X | X | – | – | – | – | X | X | – | – | – |
| Total 9 (6 *sp. nov.*) | 5(0) | 4(2) | 0 | 0 | 0 | 0 | 5(1) | 5(1) | 0 | 0 | 0 |
| Biogeographical realms | Nearctic | | Oceania | Neotropics | Antarctica | Afrotropic | Palearctic | | Indo-Malay | | Australasia |
| Total 9 (Endemics) | 7(2) | | 0 | 0 | 0 | 0 | 7(2) | | 0 | | 0 |

an arctic taxon not included in the present study, was recently found to represent a further species in the *hymenina* group (McMullin & Miadlikowska 2022).

### *Infraspecific taxa recognised in section Polydactylon*

The subspecies rank (sensu Hawksworth 1974) was formally recognised within the *Peltigera polydactylon* lineage (Magain et al. 2016), to acknowledge an intermediate level of genetic variation discovered in Central and Eastern Asia for otherwise genetically well-segregated monophyletic clades of *P. polydactylon* subsp. *polydactylon* and subsp. *udeghe*.

Additionally, we discovered that *P. dissecta* (Purvis & James 1993) restricted to the Azores archipelago (North Atlantic) represents a morphotype of *P. hymenina*, which displays an interesting phenotypic pattern in this area. Large and robust populations easily identified as *P. hymenina* (*P. hymenina* var. *hymenina*) thrive on mossy roadbanks and old walls but are rarely found at the base of trees in degraded laurisilva whereas smaller thalli with a typical pale bluish (to almost white) color when wet and distinct morphological features (e.g., presence of numerous folioles; see description of *P. hymenina* below for more details) are abundant on tree trunks and branches of various size (*P. hymenina* var. *dissecta*). None of the species delimitation methods used by Magain et al. (2017b) recognised these morphologically and ecologically distinct populations at the species level. However, we decided to recognise these specimens at the variety level since the dissecta morphotype is easily recognised and has a different ecology from typical *hymenina* (it always grows on trunks or branches of trees vs soil and rocks).

Despite support for the recognition of three putative species within *P. kukwae* (depending on the priors of the BPP analyses), due to limited material we introduce a single species with its phyllidiate morphotype recognised at the infraspecific level (var. *phyllidiata*).

Three collections of *P. truculenta* with a distinctly scabrous upper surface, a feature which is unusual for this species, have a unique ITS haplotype and are resolved as a well-supported lineage sister to the remaining accessions of *P. truculenta*. Owing to their phylogenetic position and unique morphology in their geographic context (the scabrous specimens are restricted to Chile and Gough Island), we recognise this lineage as *P. truculenta* var. *austroscabrosa*.

In the first two cases, the variety level was chosen to depict the fact that specimens did not cluster into two monophyletic clades, such as the two subspecies within *P. polydactylon* (Magain et al. 2016). We also chose the variety level for the two clades within *P. truculenta* because their monophyly was recovered based on few specimens and loci, and the support for a monophyletic *P. truculenta* var. *truculenta* is low (Fig. 2). The subspecies rank could be proposed if this result is corroborated by future evidence.

### *Main morphotypes*

The few morphological characters with a taxonomical value available across the genus *Peltigera* can be variable within and among species (Holtan-Hartwig 1993, Goffinet & Hastings 1994, Goffinet et al. 1994, Vitikainen 1994a, 1998) and highly homoplasious as demonstrated by molecular inferences. Within the genus, very few species display morphological traits that are autapomorphic, e.g., granular to flattened isidia typical for *P. evansiana*, peltate isidia unique to *P. lepidophora*, reticulate and foveate veining pattern on the lower thallus surface diagnostic for *P. retifoveata*, and small green thalli with a single

**Table 3** Distribution of morphotypes among species of dolichorhizoid and scabrosoid clades.

| Morphotypes | dolichorhiza | hymenina | neopolydactyla | occidentalis | polydactylon | pulverulenta | scabrosa | stanleyensis |
|---|---|---|---|---|---|---|---|---|
| ***hymenina* group** | | | | | | | | |
| *elixii* | present | – | – | – | present | – | – | – |
| *gallowayi* | present | – | present | – | present | – | – | – |
| *hawaiiensis* | present | – | – | – | present | – | – | – |
| *hymenina* | – | present | present | – | – | – | – | – |
| *hymenina* var. *dissecta* | – | present | – | – | – | – | – | – |
| *stanleyensis* | – | – | – | – | – | – | – | present |
| ***dolichorhiza* group** | | | | | | | | |
| *dolichorhiza* | present | – | present | – | – | – | – | – |
| *itatiaiae* | present | present | – | | – | – | – | – |
| *kukwae* | present | – | present | – | – | – | – | – |
| *kukwae* var. *phyllidiata* | present | – | present | – | – | – | – | – |
| *massonii* | – | – | – | | – | – | – | present |
| *pulverulenta* | – | – | – | | – | present | – | – |
| *sipmanii* | – | – | – | | – | present | – | – |
| *truculenta* | – | present | – | present | – | | – | – |
| *truculenta* var. *austroscabrosa* | – | – | – | | – | present | – | – |
| *willdenowii* | – | – | – | | – | present | – | – |
| ***pacifica* group** | | | | | | | | |
| *appalachiensis* | – | | present | – | – | – | – | – |
| *asiatica* | present | – | – | – | present | – | – | – |
| *borinquensis* | present | – | – | – | – | – | – | – |
| *mikado* | present | – | – | – | present | – | – | – |
| *pacifica* | – | – | present | – | – | – | – | – |
| *vitikainenii* | – | – | present | – | – | – | – | – |
| ***occidentalis* subclade** | | | | | | | | |
| *esslingeri* | – | – | present | present | – | | – | – |
| *occidentalis* | – | – | present | present | – | | – | – |
| *orientalis* | – | – | present | present | – | | – | – |
| ***scabrosella* subclade** | | | | | | | | |
| *flabellae* | – | – | present | – | – | – | – | – |
| *hokkaidoensis* | – | – | – | – | present | – | – | – |
| *scabrosella* | – | – | – | – | – | – | present | – |
| ***melanorrhiza* subclade** | | | | | | | | |
| *chabanenkoae* | – | – | present | present | – | – | – | – |
| *melanorrhiza* | present | – | – | – | – | – | – | – |
| *nigriventris* | – | – | present | – | – | – | – | – |
| ***scabrosa* subclade** | | | | | | | | |
| *borealis* | – | – | – | – | – | – | present | – |
| *clathrata* | – | – | present | – | – | – | – | – |
| *holtanhartwigii* | – | – | – | – | – | – | present | – |
| *neopolydactyla* | – | – | present | – | – | – | – | – |
| *rangiferina* | – | – | – | – | – | – | present | – |
| *scabrosa* | – | – | – | – | – | – | present | – |

**Fig. 4** a–c. Examples of dolichorhiza morphotype. a, b. *Peltigera dolichorhiza* from Rwanda. a. *E. Sérusiaux* s.n. Sept. 2006, LG; b. *E. Sérusiaux* s.n. Mar. 2005, LG; c. *Peltigera mikado* from Taiwan (*E. Sérusiaux* T103, LG); d. comparison of two different morphs of *P. asiatica*, top: dolichorhiza morphotype (*E. Sérusiaux* T69 w. *B. Goffinet* from Taiwan, LG), bottom: polydactylon morphotype (*E. Sérusiaux* T299 from Taiwan, LG).

**Fig. 5** a. Example of hymenina morphotype (*P. hymenina* from La Palma, *E. Sérusiaux* DNA1969, LG); b–d. examples of neopolydactyla morphotype; b, c. *Peltigera neopolydactyla* from Norway (*R. Haugan* 6102, O); d. *Peltigera clathrata* from Oregon (*B. McCune* 26977, OSC).

**Fig. 6** a, b. Example of polydactylon morphotype (*Peltigera polydactylon* from Switzerland, *E. Sérusiaux* s.n. 2018, LG); c, d. examples of occidentalis morphotype (*Peltigera occidentalis* from Norway, *S. Rui* 9145, O).

**Fig. 7** a. Example of stanleyensis morphotype (*Peltigera stanleyensis* from Papua New Guinea, *E. Sérusiaux* DNA1545, LG); b. example of scabrosa morphotype (*Peltigera rangiferina* from Alaska, *R. Rosentreter* 18621, OSC); c, d. examples of pulverulenta morphotype (*Peltigera pulverulenta* from Colombia, *D. Fonseca* & *F. Martinez* 214, UDBC).

attachment and marginal rounded apothecia found only in *P. venosa*. In the entire section *Polydactylon*, the occurrence of soralia in *P. weberi*, a very rare species endemic to Papua New Guinea (Sérusiaux et al. 2009) is the only example of an autapomorphic morphological character. *Peltigera weberi* was not included in the molecular analyses (lack of multilocus data) but based on its ITS sequence it belongs to the *nana* group within the polydactyloid clade.

Eight morphotypes were defined to accommodate the morphological spectrum observed in section *Polydactylon* (Table 3; Fig. 4, 5, 6, 7).

The dolichorhiza morphotype (Fig. 4a–c)
is characterised by a thin and brittle thallus with an undulating upper surface and shallow irregular concave cavities grading almost to scrobiculate; lower surface is pale near the lobe margins with distinct white elliptical interstices defined by a network of flat or slightly raised, usually dark veins; rhizines are simple and long. Populations from tropical areas or the southern hemisphere with this morphotype have almost always been identified as *P. dolichorhiza* (Swinscow & Krog 1988, Vitikainen 1998, Galloway 2007, Louwhoff 2009, Kukwa et al. 2014), but molecular inferences clearly demonstrate that many of them represent different lineages within the dolichorhizoid clade (Magain et al. 2017a, b) often intermixed with species of the pulverulenta and hymenina morphotypes. Conversely, but rarely, some populations with quite robust and thick thalli from the Neotropics belong to *P. dolichorhiza.*

The hymenina morphotype (Fig. 5a)
is characterised by pale (pale yellow or orange to almost white) marginal parts of the lower thallus surface with hardly visible veins and interstices, which can become better defined towards the center. *Peltigera hymenina* itself may have a very different lower surface with a strong contrast between black veins and pale interstices, exceeding to the margin of the lobes (Clarke 2016).

The neopolydactyla morphotype (Fig. 5b–d)
is very similar to the dolichorhiza morphotype, with the main difference in the 'toughness' of the thallus: fragile specimens belong to the dolichorhiza morphotype whereas robust specimens represent the neopolydactyla morphotype. The rhizines in both morphotypes are usually long and simple. Populations with this morphology in temperate-boreal areas of both hemispheres have generally been identified as *P. neopolydactyla* (Holtan-Hartwig 1993, Goffinet & Hastings 1994, Vitikainen 1994a, Goward et al. 1995, Galloway 2007).

The polydactylon morphotype (Fig. 6a, b)
has a characteristic lower surface, which is usually pale (whitish to pale orange) near the lobe margins and becoming darker towards the center; veins are variable, ranging from almost flat to distinctly raised and convex, forming a distinct pattern with large, numerous, elliptical or rounded interstices, which typically become smaller and often less defined towards the margins because of the denser vein network. A cream-colored or brownish orange araneous hyphal layer develops over the veins and the interstices, which is well visible especially at the margins. The polydactylon morphotype is widespread amongst the species in the polydactyloid clade, but it was also observed in several species of the two remaining clades in the section. Interestingly, two new species, *P. asiatica* and *P. mikado*, both endemic to Eastern Asia and resolved as sister to *P. pacifica* (Fig. 2), display the polydactylon morphotype with patches of scattered, minute whitish crystals on their upper surface, a feature mostly represented in the polydactyloid clade (e.g., in *P. nana*, *P. oceanica* and *P. weberi* from Papua New Guinea; Sérusiaux et al. 2009) and outside of the section *Polydactylon*. These two species can develop two different morphotypes (dolichorhiza and polydactylon types), which are sometimes found in the same locality.

The occidentalis morphotype (Fig. 6c, d)
has a lower surface with features of the hymenina morphotype because of the pale yellow color near the lobe margins and of the polydactylon morphotype because of the numerous elliptical or rounded interstices, which become smaller towards the lobe margins due to denser vein network. Despite these similarities, it is easily recognised by its highly contrasted lower surface, in which the flat or slightly raised veins are pale towards the margins, becoming dark and soon blackish with small white interstices towards the center. The rhizines are typically fasciculate and brush-like.

The stanleyensis morphotype (Fig. 7a)
is characterised by a brittle thallus with a dark brown shiny slightly undulating upper surface and a lower surface with flat broad dark veins with almost no interstices. This peculiar morphotype is found in two species: *P. massonii* belonging to the *dolichorhiza* group and *P. stanleyensis* belonging to the *hymenina* group (Fig. 2).

The scabrosa morphotype (Fig. 7b)
is characterised by a scabrous upper surface of the thallus and refers to populations occurring in boreal and arctic biomes, as well as in mountain ranges of the northern hemisphere. Lower surface can vary in this morphotype and provide helpful but not clear-cut characters to differentiate the four species: *P. borealis*, *P. holtanhartwigii*, *P. rangiferina* and *P. scabrosa.*

The pulverulenta morphotype (Fig. 7c, d)
is characterised by a scabrous upper surface (similar to the scabrosa morphotype) and a lower surface with abundant rhizines, which are very short near the margins and becoming quite long towards the thallus center, forming usually dense mats. This morphotype is confined to the New World, from Mexico to Southern South America. Thalli of the pulverulenta morphotype usually have narrower, more elongated lobes than the scabrosa morphotype.

### *Correspondence between molecular and phenotypic data*

Many newly delimited species in section *Polydactylon*, although phylogenetically well circumscribed and representing independent lineages (Magain et al. 2017a, b), cannot be confidently recognised without DNA sequences, which is a common pattern reported in other lichen groups, e.g., in *Bryoria*, *Rhizoplaca*, *Xanthoparmelia* (Lumbsch & Leavitt 2011, Leavitt et al. 2018, Boluda et al. 2019).

However, for several *Peltigera* species their evolutionary distinctness was corroborated by at least one other character, i.e., morphology, secondary metabolites, geographical distribution or *Nostoc* identity. For example, three species: *P. elixii*, *P. gallowayi* and *P. hawaiiensis* from the poorly resolved *hymenina* group within the *dolichorhiza/hymenina/pacifica* subclade were collected along the western fringe of the Pacific. *Peltigera elixii* displays the dolichorhiza morphotype, produces a unique set of terpenoids, and is endemic to Papua New Guinea. *Peltigera hawaiiensis* has a variable morphology and lacks diagnostic chemical features, but it is the only representative of section *Polydactylon* in the Hawaiian island archipelago. *Peltigera gallowayi* has a very variable morphology (dolichorhiza, neopolydactyla and polydactylon morphotypes), and also lacks diagnostic chemical characters, but it is restricted to Australia and New Zealand. Locally this species is easily distinguished by the absence of characters that are diagnostic for the other two species from section *Polydactylon*, present in this area: pruinose upper surface of the thallus margins with occasional large and conspicuous laminal incrustation patches typical for *P. nana* (Sérusiaux et al. 2009), and undulate, crisped and usually phyllidiated thallus margins typical for *P. polydactylon* subsp. *udeghe* (Magain et al. 2016).

Morphospecies recognised in Europe and complemented by sets of secondary metabolites (Holtan-Hartwig 1993, Goffinet et al. 1994, Vitikainen 1994a) cannot be applied to disentangle taxonomy of *Peltigera* worldwide. In the European context, the combination of morphology and occurrence of certain terpenoids remains sufficient to distinguish *P. hymenina* and *P. neckeri* from *P. polydactylon*, *P. aphthosa* from *P. leucophlebia*, *P. horizontalis* from *P. elisabethae*. *Peltigera seneca* was recently found in Norway and Finland, where it cannot be morphologically distinguished from *P. polydactylon*, but the two species can be segregated by their different TLC profiles (Timdal & Rui 2021).

However, the morpho-chemical species concept cannot be successfully applied in several other cases, e.g., to distinguish species with the morphotypes of *P. neopolydactyla* and *P. scabrosa.* European *P. neopolydactyla* sensu Vitikainen (1994a) encompasses four species belonging to two different clades within section *Polydactylon*, whereas *P. scabrosa* s.lat. represents a complex of four species (*P. scabrosa* s.str., *P. borealis*, *P. holtanhartwigii* and *P. rangiferina*) in the *scabrosa* subclade. As currently defined, the European morphospecies cannot accommodate the large genetic diversity discovered in other areas, especially in Northwestern North America, in the Andes and in Eastern Asia. For example, Magain et al. (2017a, b) resolved with strong support the placement of the *P. neopolydactyla* morphotype in 11 different lineages across two main clades (dolichorhizoid and scabrosoid). A similar situation was found in section *Peltigera* where widely accepted species such as *P. canina*, *P. degenii* and *P. rufescens* turned out to represent species complexes strongly supported by molecular data, and often with distinct patterns of distribution yet morphologically cryptic (Jüriado et al. 2017, Magain et al. 2018).

It is also quite common that different morphotypes (defining morphospecies sensu Holtan-Hartwig 1993, Vitikainen 1994a, 2007) were found to be present within a single evolutionary lineage, which was often recognised as a single species by molecular inferences. For example, *P. asiatica*, *P. mikado* and *P. gallowayi* can develop either the dolichorhiza or the polydactylon morphotype, and the latter species can also have the neopolydactyla morphotype. Large morphological variation was also observed in *P. truculenta* and *P. dolichorhiza* s.str., typically with dolichorhiza morphotype, but sometimes also developing the neopolydactyla morphotype.

The development of different morphotypes within a single evolutionary lineage is an emerging issue in lichen biology and worthy of further investigations, especially when two different morphotypes thrive side by side, as observed in Taiwan for *Peltigera asiatica* and *P. mikado.* A similar scenario has recently been documented for two *Sticta* species in New Zealand (Lücking et al. 2021).

The color of the thallus can sometimes be useful to identify species in the field. In boreal forests and alpine-arctic biomes, mycobionts associating with *Nostoc* from phylogroup VIIa form thalli of emerald green color when wet, contrary to grey or brown thalli of species associated with other *Nostoc* phylogroups. For example, in the boreal region, *P. appalachiensis* and *P. occidentalis* can be distinguished from *P. neopolydactyla* and *P. vitikainenii* by their emerald green color (Fig. 8c). However, it can be misleading because of switches from one *Nostoc* phylogroup to another as documented in *P. appalachiensis* and *P. occidentalis*, which form grey or brown thalli in temperate regions of North America where they associate with *Nostoc* phylogroup VIIb and VIIc (Fig. 8d; Magain et al. 2017a, b). This represents a phenomenon analogous to photomorphs where the same fungus forms different thallus with a cyanobacterium or alternatively with a green alga (e.g., Tønsberg & Holtan-Hartwig 1983, Ott 1988, Armaleo & Clerc 1991, Goffinet & Bayer 1997, Magain et al. 2012, Moncada et al. 2013a). A similar switch in symbionts affecting thallus morphology (pannarioid vs collematoid) was demonstrated in *Fuscopannaria* (*Pannariaceae*, *Peltigerales*; Magain & Sérusiaux 2014, 2015b) and it is suspected to occur in the complex assemblage of *Lepidocollema* and *Physma* (Ekman et al. 2014, Magain & Sérusiaux 2014). It should be noted that emerald green thalli can be present in other species within the genus *Peltigera*, e.g., in *P. islandica* from section *Peltigera* (Manoharan-Basil et al. 2016) and in several species from section *Peltidea*, associated with different phylogroups of *Nostoc*.

Because of the lack of consistent and reciprocal genotype-morphotype correspondence at the species level, reliable species identification in section *Polydactylon* (and the entire genus *Peltigera*) cannot rely solely on morphological and chemical characters. Due to common cases of strong phenotypic variation, convergence (e.g., scabrous upper thallus surface present in phylogenetically unrelated clades) or retention of ancestral traits (e.g., neopolydactyla morphotype spread across the entire section *Polydactylon*), to properly identify material in the dolichorhizoid and scabrosoid clade in section *Polydactylon* the ITS sequences are needed. Every species described in section *Polydactylon* can be confidently identified by its ITS sequence (Fig. 9).

Recently, new species of lichen-forming fungi have been described on the sole basis of DNA, e.g., in *Lepraria* (Lendemer 2011) and *Parmelia* (Molina et al. 2011). Although it has been argued that concise diagnoses and/or DNA-only diagnoses rather than complete and detailed descriptions may speed up taxonomical duty (Leavitt et al. 2016b, Renner 2016), we also provide complete and classic descriptions of all species, including species for which a validly published epithet is available. We follow the rationale of the rules edited by Tripp & Lendemer (2014) to avoid describing new species with DNA-only diagnostic characters.

### *Ascospore morphology*

Three main types of ascospores (all described as acicular in Holtan-Hartwig 1993 and Vitikainen 2007) were recognised in the examined material (Fig. 10): a) rather narrow and elongated fusiform ascospores, usually bent or slightly flexuose; b) larger, almost cylindrical and either bent or straight ascospores; and c) very long and narrow ascospores, remaining straight or flexuose. In general, all examined ascospores were narrow and rather long, in some species over 100 µm long, but their ends were never acute, and instead always rounded. According to the botanical definition of the acicular shape (https://www.vocabulary.com/dictionary/acicular) described as 'narrow, long and pointed', the last characteristic does not apply to ascospores found in *Peltigera* section *Polydactylon*.

In several subclades, ascospores across species are identical or very similar. This is the case with the following subclades: occidentalis (three species, but in *P. esslingeri* no mature spores were observed); scabrosella (three species); melanorrhiza (three species but in *P. nigriventris* no mature spores observed); scabrosa (six species but in three: *P. holtanhartwigii*, *P. clathrata* and *P. rangiferina* no mature spores were observed). In contrast, within the *dolichorhiza* subclade, the ascospores of *P. pulverulenta* strongly differed from those of *P. dolichorhiza*, *P. kukwae* and *P. truculenta*; within the *hymenina* subclade, the ascospores of *P. elixii*, *P. gallowayi* and *P. hawaiiensis* are much smaller than those of *P. hymenina* (incl. var. *dissecta*) and *P. stanleyensis*. Within the *pacifica* group, the ascospores of both species from East Asia (*P. asiatica* and *P. mikado*)

**Fig. 8** Pictures of selected *Peltigera* species in the field. a. *Peltigera hymenina* in Tenerife; b. *Peltigera vitikainenii* in Vosges, France; c. differences in color thalli between *Peltigera neopolydactyla* (left) and an emerald green thallus with phylogroup VIIa (right, *P. occidentalis* or *P. appalachiensis*); d. *Peltigera appalachiensis* in North Carolina, USA, with phylogroup VIIb and a grey thallus.

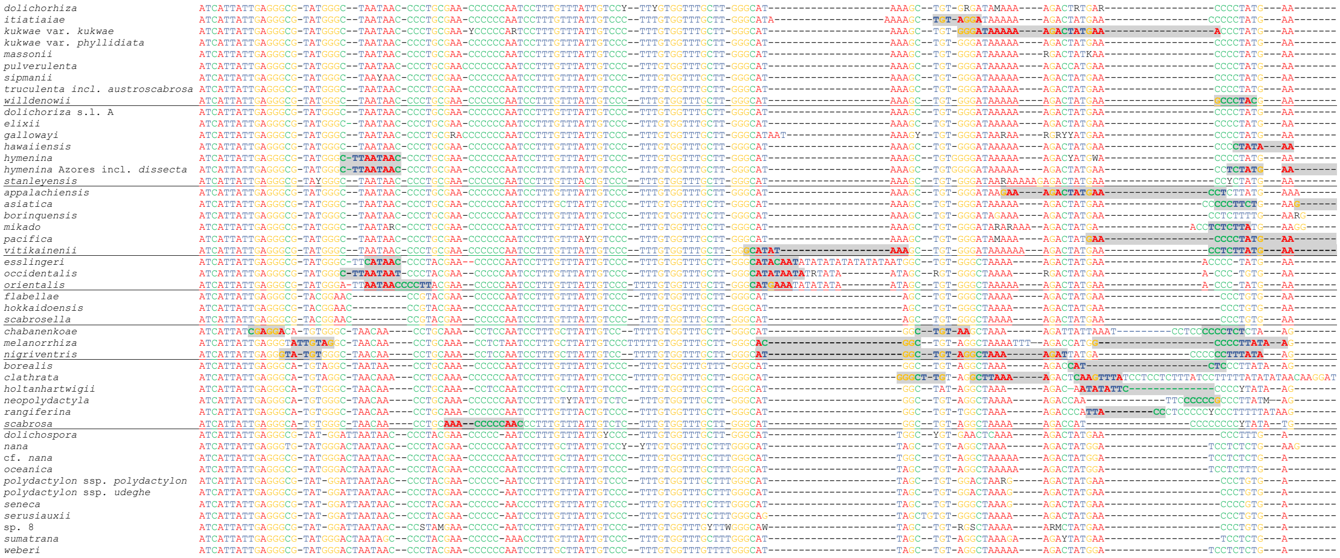

**Fig. 9** Consensus sequences of ITS1 and ITS2 including IUPAC ambiguity symbols for polymorphic positions, with highlighted barcodes selected for molecular identification of each species recognised in this study. Order of species follows the order of the section 'species description', clade by clade, then alphabetical order within clades. Barcodes are highlighted in grey. Each barcode is unique to the recognised species even when several barcodes are provided for one species.

**Fig. 9** (cont.)

**Fig. 9** (cont.)

**Fig. 9** (cont.)

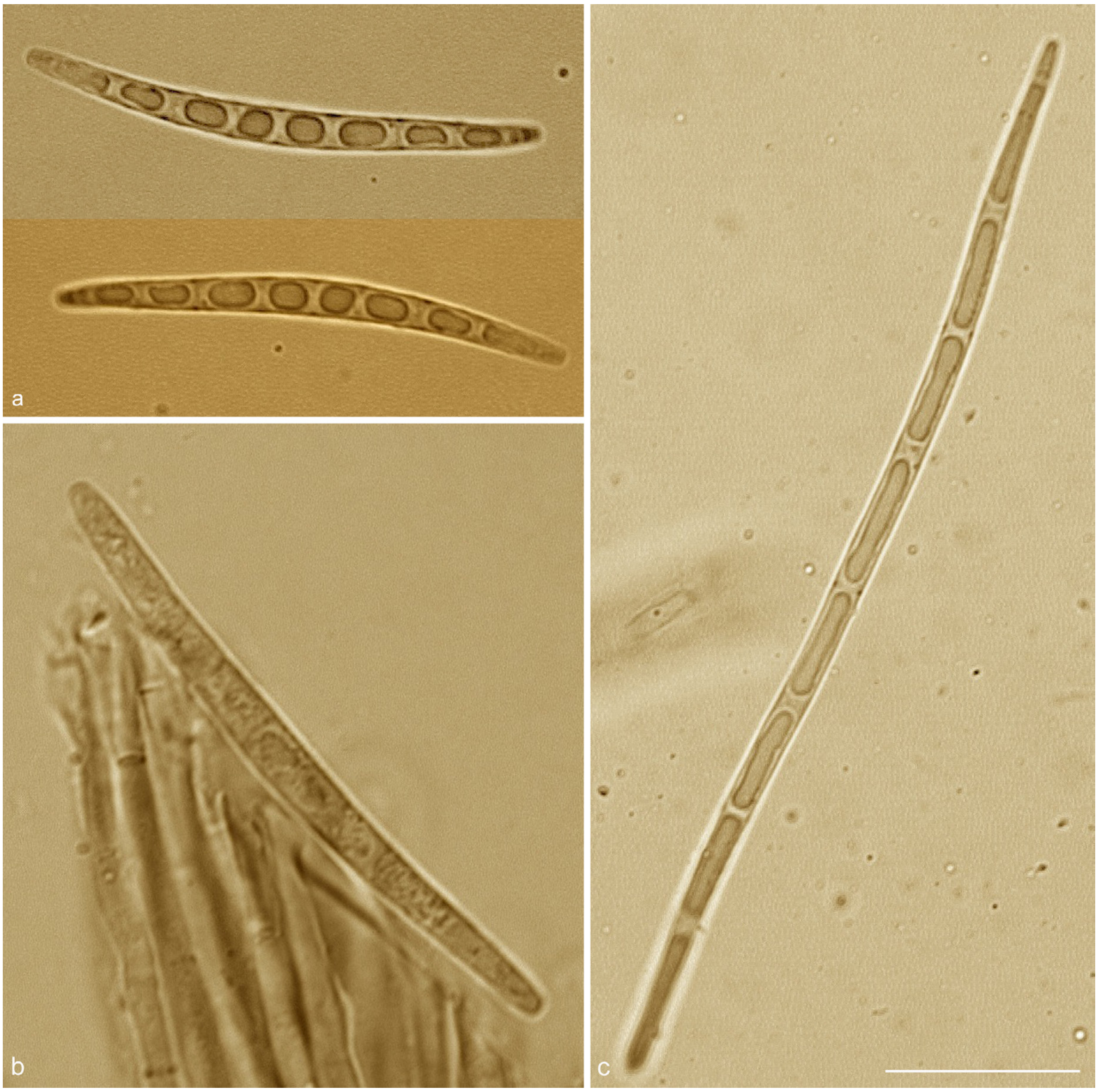

**Fig. 10** Main types of ascospores found in *Peltigera* section *Polydactylon*. a. Ascospores of *P. gallowayi*: narrow and elongated, fusiform, slightly bent (New Zealand, *R. Lücking*, *B. Moncada* & *P. de Lange* 39039, F); b. ascospores of *P. dolichorhiza*: relatively large and almost cylindrical, bent (Rwanda, *E. Sérusiaux* s.n., 2010, LG); c. ascospores of *P. borealis*: very long, narrow and flexuose (Canada, Québec, *J. Miadlikowska* & *F. Lutzoni*, DNA-P5033, DUKE).

strongly differ in shape and size from the remaining species. No ascospore traits could be recognised as autopomorphic for any of the species as delimited in this work.

### *Nomenclature and typification of validly published epithets*

Many specific or infraspecific epithets have been validly published within the genus *Peltigera* (see Holtan-Hartwig 1993, Vitikainen 1994a). Four epithets have been widely used for populations of the four eponym morphotypes: dolichorhiza (*P. dolichorhiza*), neopolydactyla (*P. neopolydactyla*), pulverulenta (*P. pulverulenta*) and scabrosa (*P. scabrosa*). Based on molecular data, Magain et al. (2017a, b) demonstrated that these morphotypes were highly homoplasic and were not diagnostic of monophyletic groups.

Epitypification is a provision of the International Code of Nomenclature for algae, fungi, and plants, Art. 9 (Turland et al. 2018), and can be used following strict guidelines. Designating an epitype is appropriate to interpret type material that cannot be confidently assigned to a modern concept of a species (Ariyawansa et al. 2014). Epitypification has been increasingly applied in lichen taxonomy. Examples can be found in nomenclatural revisions of forgotten names (Laundon 1984, Lücking et al. 1998) or in integrative approaches to species complexes (Alors et al. 2016, Gasparyan et al. 2017, Lücking et al. 2017b). In this study, we applied epitypification to fix the application of the widely used epithets *P. dolichorhiza* and *P. pulverulenta*, following the rules edicted by Lendemer (2020).

The type collection of *P. dolichorhiza* (from Colombia) was examined by Galloway (1985) and Vitikainen (1998) and it matches the dolichorhiza morphotype and its most frequent chemotype containing tenuiorin, methylgyrophorate, peltidactylin, dolichorrhizin and zeorin. In our opinion, this collection matches the features of the specimens from the most abundant and widespread lineage found in the montane forests of the Andes in Central and northern South America (including Colombia) (Magain et al. 2017b; Fig. 2). However, several species newly described in South America have very similar morpho-chemical descriptions and therefore require ITS sequences for a reliable identification. To avoid any confusion, we choose to epitypify *P. dolichorhiza* with a recent collection from Colombia.

In addition to *P. pulverulenta* (type collection from Ecuador; not Colombia as mentioned by Vitikainen 1998), two epithets are available to accommodate three species recognised within the *P. pulverulenta* s.lat. complex (Magain et al. 2017a, b): *P. micro-*

*dactyla* (from Venezuela), and possibly *P. pulvinascens* (from Ecuador). Vitikainen (1998) recognised *P. microdactyla* as a separate morphospecies defined by a thin thallus and a distinct venation pattern compared to *P. pulverulenta*. However, molecular data do not support the recognition of this morphotype as a distinct species. All putative species within *P. pulverulenta* s.lat. form a single, strongly supported lineage and are mostly sympatric, with one of them being widespread and relatively common. Therefore, we epitypify the epithet *pulverulenta* with a collection from Ecuador belonging to this lineage. Populations from the southern parts of Argentina and Chile with a scabrous upper surface belong to *P. truculenta* var. *austroscabrosa*, a new variety proposed here. We chose not to use the epithets *microdactyla* and *pulvinascens* to accommodate the two other species because their types likely belong to the more abundant *P. pulverulenta* s.str. rather than the two rare new species.

Four chemotypes (I–IV) and three morphotypes (A, B and C) were distinguished within populations referred to as *P. neopolydactyla* in Norway (Holtan-Hartwig 1993). This variation was confirmed at a broader geographic scale in Europe (Vitikainen 1994a) and British Columbia in Canada (Goward et al. 1995). Morphotype A (thallus thick and rigid, emerald green when wet, with bush-shaped, medium long rhizines) *sensu* Holtan-Hartwig (1993) was previously recognised as a distinct species, under the name *P. occidentalis* (Goward et al. 1995, Miadlikowska & Lutzoni 2000, Vitikainen 2007) and retained in this study. Morphotype B (thallus thin, greyish blue when wet, with long, slightly branched rhizines) and morphotype C (thallus medium thick, greyish brown when wet, with bush-shaped to slightly branched, medium long rhizines) and their corresponding three chemotypes were resolved in multiple lineages scattered across the dolichorhizoid and scabrosoid clades (Magain et al. 2017b). The type collection of *P. neopolydactyla* originates from Sweden and represents chemotype IV (with zeorin as the only terpenoid detected) of Holtan-Hartwig (1993) and morphotype B or C. The lineage referred to as *P. neopolydactyla* 4 in the scabrosoid clade (Magain et al. 2017a, b) matches the type characteristics and most likely occurs in Sweden as it was found in Norway and Finland, therefore the epithet *neopolydactyla* was assigned to this well delimited clade, obviating the need for epitypification.

The lectotype collection for *P. scabrosa* (Vitikainen 1994a) originates from Greenland and represents the most common chemotype I (Holtan-Hartwig 1993) containing three main terpenoids (peltidactylin, dolichorrhizin and zeorin). DNA sequences from the lectotype could be obtained and confirm that it corresponds to *P. scabrosa* 2, which displays this chemotype.

We did not assess the numerous epithets published as infraspecific levels, because most of them have never been used and many are based on poor and old material, or collections that are impossible to locate in herbaria. The only exception is *P. polydactyla* var. *conjungens* because it was suspected that the type collection (from Australia) could correspond to the most common species in section *Polydactylon* in Australia and New Zealand, the newly described *Peltigera gallowayi*. However, sequencing of the type revealed that *P. polydactyla* var. *conjungens* corresponds to *P. polydactylon* subsp. *udeghe*, a taxon already reported in Australia and New Zealand (Magain et al. 2016). Synonymy of these two names is proposed below.

### *Biogeographic patterns*

*Peltigera* is one of the very few lichen genera for which the world-wide distribution patterns of a large number of species have been summarized and analyzed (Martínez et al. 2003). The authors assigned each of the 66 morphospecies to six biogeographic kingdoms (Holarctic, Neotropical, Paleotropical, Australian, Holantarctic and Cape), 40 regions and 230 provinces following Takhtajan et al. (1986). The Holarctic Kingdom was found to harbor the highest number of *Peltigera* species including the highest number of endemic species.

Molecular phylogenetic revisions and inventories performed on various groups of *Peltigera* at different biogeographic scales, and more recently using multiple species delimitation and validation methods (O'Brien et al. 2009, 2013, Sérusiaux et al. 2009, Lendemer & O'Brien 2011, Han et al. 2013, 2015, Miadlikowska et al. 2014, Ramírez-Fernández et al. 2015, Magain et al. 2017a, b) have drastically changed our understanding of the overall diversity and the geographic ranges of redelimited species within the genus. For example, Martínez et al. (2003) recognised 16 species within section *Polydactylon* whereas 43 species are currently delimited based on multilocus datasets (Fig. 1).

Globally, section *Polydactylon* represents a subcosmopolitan lineage with some internal biogeographic structure. Each of the three main clades has a distinct biogeographic history and pattern. Members of the polydactyloid clade are absent in Central and South America and occur mostly in Eastern continental Asia, Japan, the Indochina peninsula, the Indonesian archipelago, Australia and New Zealand, with at least eight species in this part of the world (including already described *P. dolichospora*, *P. nana*, *P. oceanica*, *P. serusiauxii*, *P. sumatrana* and *P. weberi*). A single clade including *P. polydactylon* (subsp. *polydactylon* and *udeghe*) and *P. seneca* extends into the Holarctic zone (Fig. 11e).

We assigned 34 species recognised in the dolichorhizoid and scabrosoid clades within section *Polydactylon* to biogeographic realms (Nearctic, Palearctic, Oceania, Afrotropic, Indo-Malay, Australasia and Antarctic) following Olson et al. (2001) (Table 2). The dolichorhizoid clade is widespread but absent from central Asia and represented by a single species in Africa, whereas the scabrosoid clade is restricted to the northern hemisphere. Here we examined the distribution pattern of each main group within these two clades (Fig. 1–3).

a) The *dolichorhiza/hymenina/pacifica* subclade has a very broad distribution as a whole, but finer biogeographic trends can be observed for each of its three groups:
    a.1) the *dolichorhiza* group (Fig. 1, 2) represents a rapid ongoing radiation mainly in Central and South America, where all potential species show a generalist symbiotic pattern (Magain et al. 2017a). It includes a strongly supported clade of taxa with a scabrous thallus upper surface (*P. pulverulenta* and related species). Whereas other species are endemic to the Neotropics, two species dispersed outside of South America: *P. dolichorhiza*, known also from montane forests in East Africa, incl. Madagascar, the Mascarene archipelago, South Africa, and the isolated island of Amsterdam in the southern part of the Indian Ocean; and *P. truculenta*, present in Chile and Argentina and reported from Gough Island (South Atlantic) and southern Kerguelen archipelago in the Indian Ocean (Fig. 11b). Similar patterns of geographic distribution were also detected in the basidiolichen genus *Cora* with an impressive radiation in Central and South America, and subsequent dispersal of two species on two islands in the South Atlantic, and another species, most probably extinct, in Mauritius (Mascarene archipelago; Lücking et al. 2015).
    a.2) the *hymenina* group is present mostly on the islands of the Pacific Ocean in Australia and New Zealand (*P. gallowayi*), Papua New Guinea (*P. elixii*, *P. stanleyensis* and *P. dolichorhiza* s.lat. A), the Philippines (one putative undescribed species) and Hawaii (*P. hawaiiensis*) (Fig. 11b). Its most widespread spe-

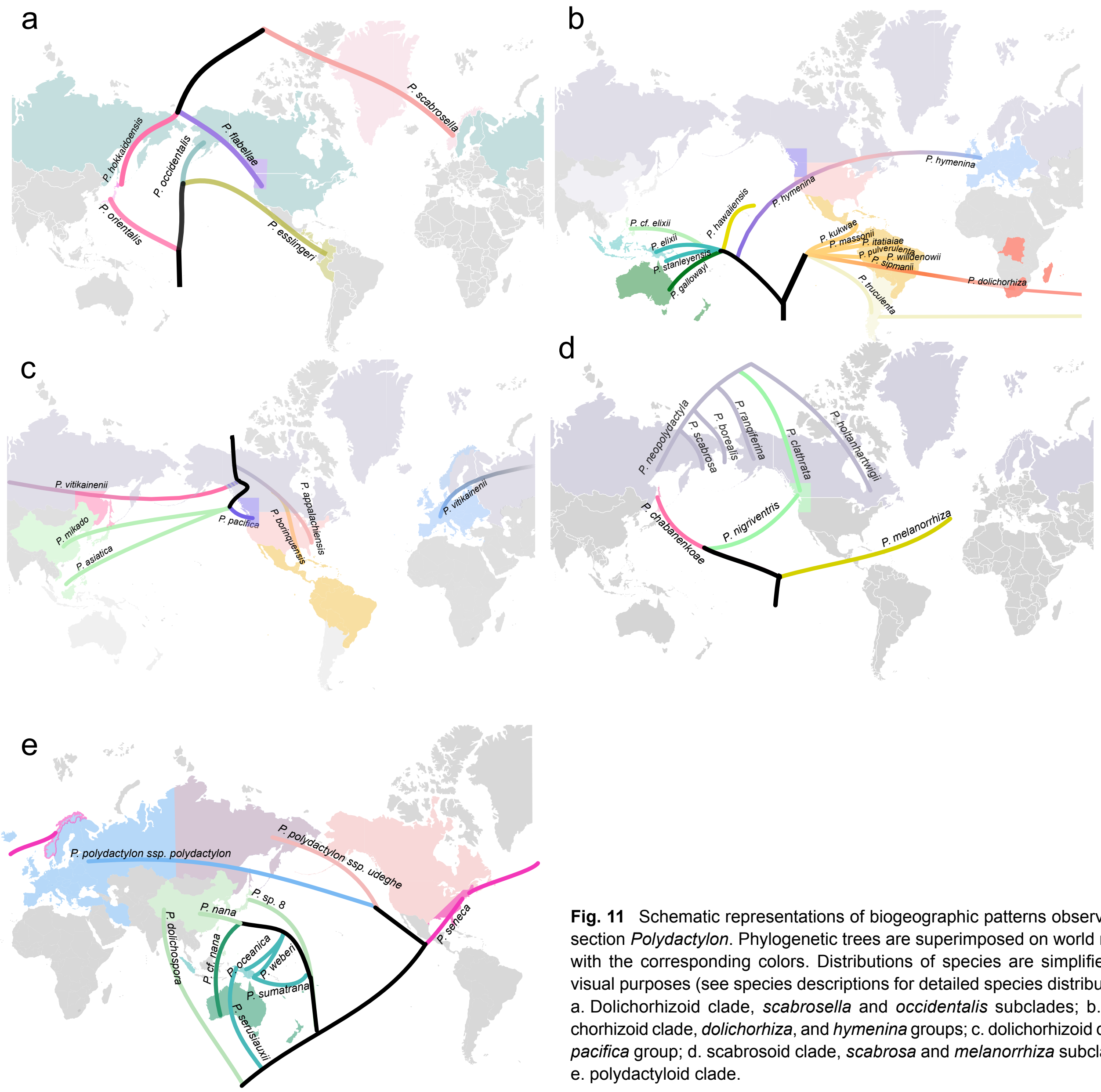

**Fig. 11** Schematic representations of biogeographic patterns observed in section *Polydactylon*. Phylogenetic trees are superimposed on world maps with the corresponding colors. Distributions of species are simplified for visual purposes (see species descriptions for detailed species distribution). a. Dolichorhizoid clade, *scabrosella* and *occidentalis* subclades; b. dolichorhizoid clade, *dolichorhiza*, and *hymenina* groups; c. dolichorhizoid clade, *pacifica* group; d. scabrosoid clade, *scabrosa* and *melanorrhiza* subclades. e. polydactyloid clade.

cies, *P. hymenina*, is known from both sides of the North American continent, as well as Macaronesia and Europe. *Peltigera lyngei*, an arctic species known from Norway/Svalbard, Iceland and USA/Alaska, was recently found to be the sister species to *P. hymenina* (McMullin & Miadlikowska 2022).

a.3) the *pacifica* group (Fig. 11c) is more diverse in the Pacific region, with *P. pacifica* in northwestern North America, two species in Eastern Asia (*P. asiatica* and *P. mikado*) and *P. vitikainenii* common in East Asia but distributed circumboreally. *Peltigera appalachiensis* has also a circumboreal distribution, but it is more widespread in Eastern North America. Its sister species, *P. borinquensis* is endemic to the Neotropics, and the only member of the *pacifica* group in that region.

b) the *occidentalis* subclade (Fig. 11a) has its eponym species present throughout the boreal zone of the northern hemisphere, with an extension in the Appalachian Mountains (USA), and two more southern species: *P. orientalis* on the main island of the Japanese archipelago and *P. esslingeri* in the Neotropics.

c) the *scabrosella* subclade (Fig. 11a) has three species restricted to relatively small territories: *P. scabrosella* in Scandinavia (mainly Norway) and Greenland, *P. flabellae* in northwest North America and *P. hokkaidoensis* in Japan.

d) the *melanorrhiza* subclade (Fig. 11d) includes three species confined to relatively small territories: *P. melanorrhiza* in the Azores, *P. nigriventris* in northwestern North America and *P. chabanenkoae* in Eastern Russia and Japan. Interestingly, the *scabrosella* and the *melanorrhiza* subclades have almost identical biogeographic patterns with one Atlantic species, one East Asian species and one northwestern North American species. Members of both groups favor oceanic conditions (mild and humid).

e) the *scabrosa* subclade (Fig. 11d) includes mostly species restricted to the boreal zone of the northern hemisphere (*P. borealis*, *P. holtanhartwigii*, *P. neopolydactyla*, *P. rangiferina*, *P. scabrosa*) but also a northwestern North American endemic (*P. clathrata*).

Species richness within the dolichorhizoid and scabrosoid clades is unevenly distributed among biogeographic zones. Eight species are widespread, mostly in boreal and arctic biomes of the northern hemisphere: *P. occidentalis*, three species with the neopolydactyla morphotype (*P. appalachiensis*, *P. neopolydactyla* and *P. vitikainenii*), and four species with the scabrosa morphotype (*P. borealis*, *P. holtanhartwigii*, *P. rangiferina* and *P. scabrosa*). Only a few species occur across the temperate biome, including the Pyrenees, the Alps and the Carpathian Mountains in Europe and the Appalachian Mountains in North America: *P. hymenina*, *P. vitikainenii* (both species can be sometimes difficult to distinguish from each other, especially in the British Isles; Clarke 2016), *P. borealis* and *P. occidentalis*, which have been confirmed or predicted to occur in temperate Europe, and *P. appalachiensis* (and *P. occidentalis*) known from the Appalachian Mountains. Interestingly, a single species, *P. dolichorhiza* s.str. was found in continental Africa, Madagascar (surprisingly known only from a single locality), and the Mascarenes archipelago.

Macaronesia has two endemic taxa: *P. melanorrhiza* and *P. hymenina* var. *dissecta*. *Peltigera melanorrhiza* is the only representative of the scabrosoid clade in Macaronesia, closely related to two newly described species (*P. nigriventris* and *P. chabanenkoae*) from the northern fringes of the Pacific Ocean (Fig. 3). Connections with northwestern North America are strongly suspected in the Macaronesian lichen flora (Tønsberg 1999, Sérusiaux et al. 2011) and have been demonstrated for plants as well (Aigoin et al. 2009, Li et al. 2011, Kondraskov et al. 2015). The other two species from section *Polydactylon* found in Macaronesia are *P. hymenina* var. *hymenina* and *P. polydactylon* subsp. *polydactylon*.

Northwestern North America is well-known for its diverse and lavish lichen biota, mainly associated with pristine forests (Goward & Arsenault 2000, McCune & Geiser 2009, Radies et al. 2009, Spribille et al. 2009, Arsenault & Goward 2016). Our study shows that section *Polydactylon* has four endemics in the region, placed in four out of the seven recognised subclades and groups (Magain et al. 2017a, b; Fig. 1): two in the dolichorhizoid clade, *P. flabellae* (*scabrosella* subclade) and *P. pacifica* (*pacifica* group) and two in the scabrosoid clade, *P. clathrata* (*scabrosa* subclade) and *P. nigriventris* (*melanorrhiza* subclade). Of these, only *P. pacifica* was previously recognised whereas the remaining three of these northwest North American endemics have the neopolydactyla morphotype and were not distinguished before ITS sequences became available. A similar situation has been recently demonstrated in Western North America for the genus *Russula* (Bazzicalupo et al. 2017). Species from six of the seven subclades of the dolichorhizoid and scabrosoid clades (the *dolichorhiza* group is missing) are present in northwestern North America. It is interesting that *P. flabellae* and *P. nigriventris* have their closest relative in Eastern Asia – *P. hokkaidoensis* (endemic to Japan) and *P. chabanenkoae* (endemic to Japan and Sakhalin Island in Russia), respectively. Eastern Asia is also the region where the three most closely related species to *P. pacifica* are exclusively found (*P. mikado* and *P. asiatica*), or where the highest haplotype diversity is present for *P. vitikainenii*.

Based on a rather limited sampling from East Asia, we detected several species or potential species complexes endemic or almost endemic to this area, such as *P.* sp. 8 and *P. dolichospora* in the polydactyloid clade. Two species endemics to East Asia, *P. asiatica* and *P. mikado* occur in Taiwan and the Yunnan province of China and are also known from Vietnam and Malaysia (for *P. asiatica*) and Japan and Eastern Russia (for *P. mikado*). Three species from three different subclades are known exclusively from Japan and East Russia: *P. orientalis*, *P. hokkaidoensis* and *P. chabanenkoae*, which co-occur in this area with three other species widespread in boreal forests: *P. neopolydactyla*, *P. occidentalis* and *P. vitikainenii*. Five of the six subclades present in northwestern North America occur also in East Russia and Japan (*hymenina* group is missing).

### Patterns in secondary compounds detected by TLC

As expected, little variation in triterpenoid composition was detected among species and species groups revealed by molecular inferences (Fig. 12, 13, 14, 15, 16, 17, 18, Tables S1, S2, Fig. S1–S10). However, several interesting patterns were detected.

All species within the *dolichorhiza* group (Fig. 12, 13) produce peltidactylin and dolichorrhizin in high quantities, and sometimes also zeorin. Dolichorrhizin is always the most abundant of the three, followed by peltidactylin then zeorin. Zeorin seems to be absent or hardly detected in *P. kukwae* (incl. var. *phyllidiata*), *P. truculenta* (incl. var. *austroscabrosa*), *P. sipmanii* and *P. willdenowii*. Tenuiorin is always abundant, whereas the amount of methylgyrophorate is highly variable. Accessory compounds

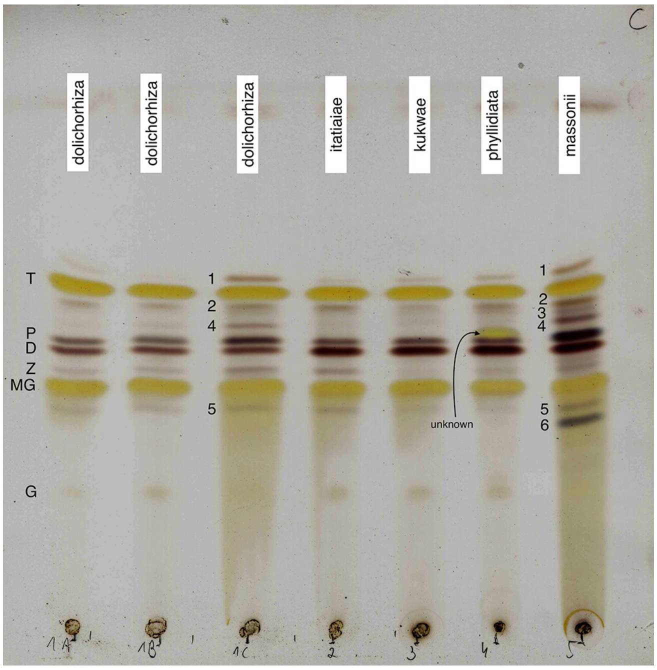

**Fig. 12** TLC in phase C for representatives of the *dolichorhiza* group in the dolichorhizoid clade. See Table S1 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

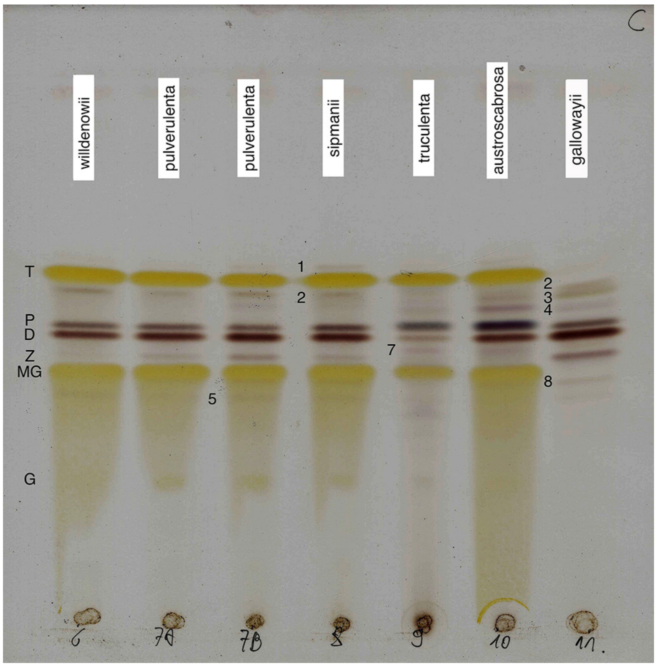

**Fig. 13** TLC in phase C for representatives of the *dolichorhiza* and *hymenina* groups in the dolichorhizoid clade. See Table S1 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

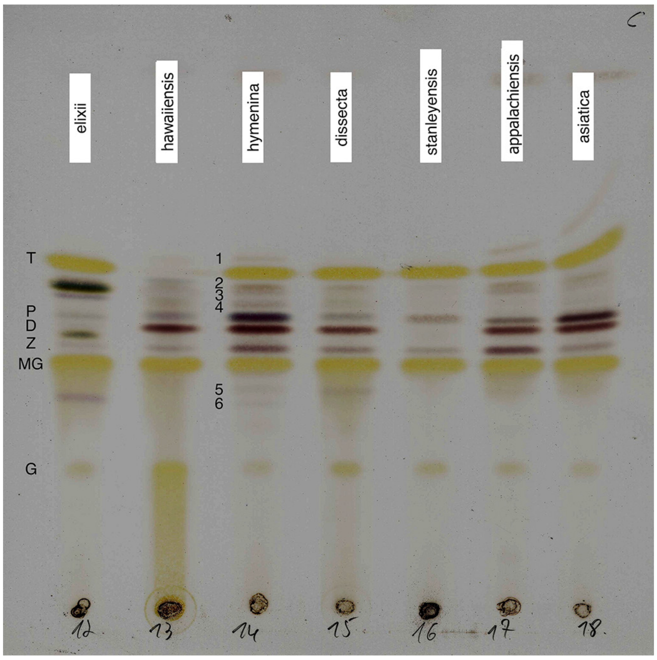

**Fig. 14** TLC in phase C for representatives of the *hymenina* and *pacifica* groups in the dolichorhizoid clade. See Table S1 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

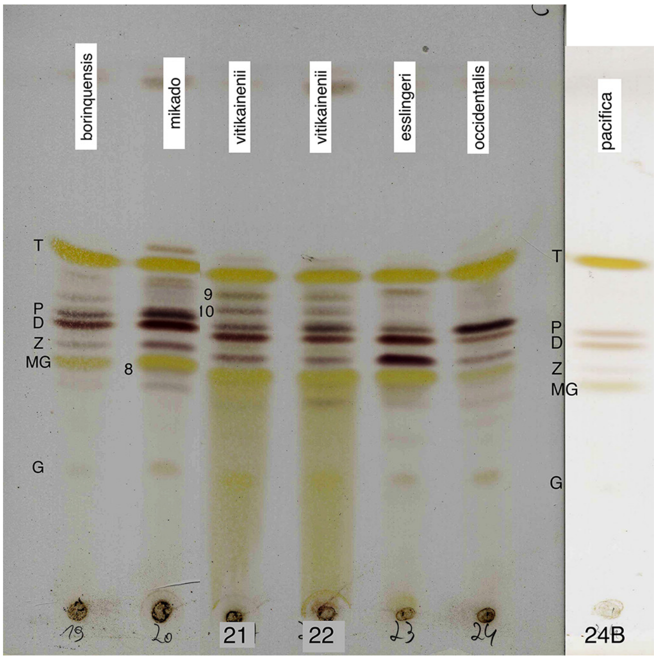

**Fig. 15** TLC in phase C for representatives of the *pacifica* group and *occidentalis* subclade in the dolichorhizoid clade. See Table S1 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

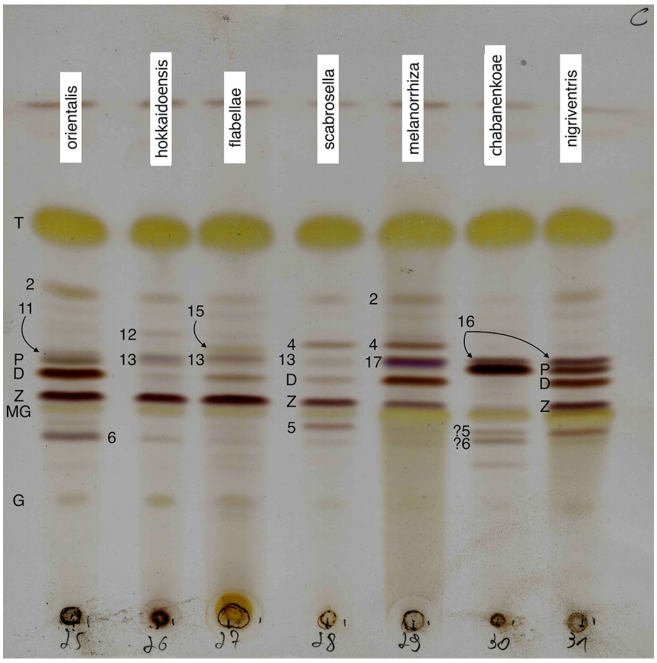

**Fig. 16** TLC in phase C for representatives of the *occidentalis* subclade and *scabrosella* subclade in the dolichorhizoid clade, and the *melanorrhiza* subclade in the scabrosoid clade. See Table S1 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

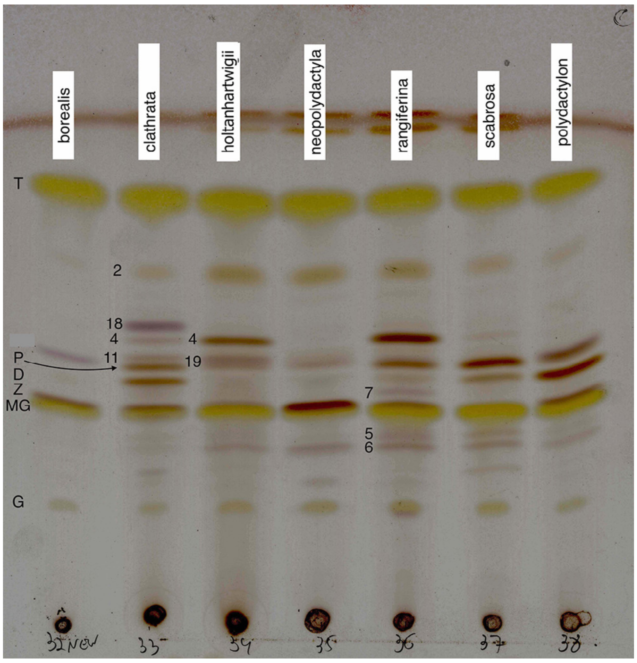

**Fig. 17** TLC in phase C for representatives of the scabrosoid and polydactyloid clades. See Table S1 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

were detected in *P. dolichorhiza*, *P. pulverulenta* and related species, and *P. massonii* (up to six accessory compounds were present). Variation is rather limited within species.

The *hymenina* group (Fig. 13, 14) is the most variable in the occurrence of the three main depsides: tenuiorin, methylgyrophorate, gyrophoric acid and the three main triterpenes: dolichorrhizin, peltidactylin, zeorin, both within and among species. *Peltigera hymenina* (incl. var. *dissecta*) is the only species in this group which contains all six secondary compounds and in addition six accessory ones. The remaining species have different patterns. In *P. gallowayi* the three depsides can be present or absent, the three triterpenes are always present and up to five accessory compounds sometimes detected. *Peltigera hawaiiensis* always has significant amounts of methylgyrophorate, and has either: a) no tenuiorin and high amounts of gyrophoric acid; or b) high amounts of tenuiorin and traces of gyrophoric acid; peltidactylin and dolichorrhizin are always present whereas zeorin, and two accessory compounds are sometimes present. *Peltigera elixii* has tenuiorin, methylgyrophorate, and gyrophoric acid and a unique set of four triterpenes always present. Two

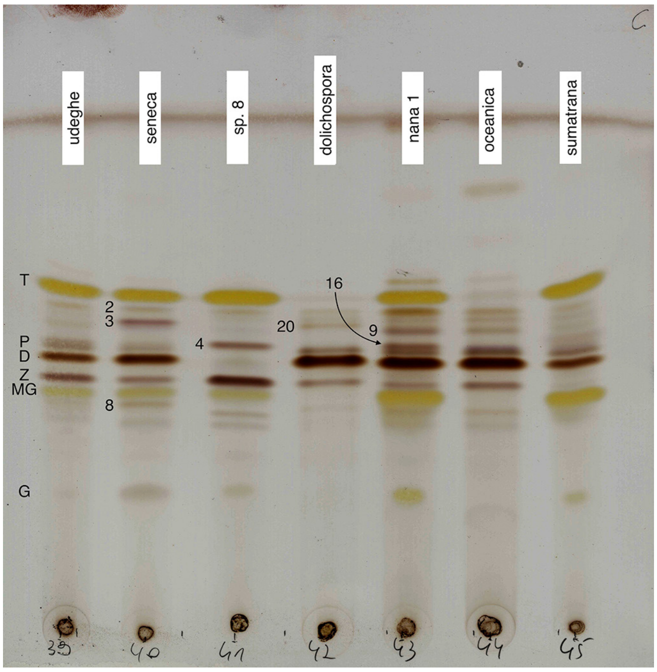

**Fig. 18** TLC in phase C for representatives of the polydactyloid clade. See Table S1 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

of these have unusual colors (bright green and red spots), which are visible for a short time just after spraying the plate with sulphuric acid and heated. *Peltigera stanleyensis* always produces zeorin and peltidactylin but never dolichorrhizin and any accessory compounds.

The *pacifica* group (Fig. 14, 15) is similar to the *dolichorhiza* group, in the presence of the three main depsides and the three main terpenes, but there is no clear pattern in relative abundance between those. The variation within *P. vitikainenii* is high.

The *occidentalis* subclade (Fig. 15, 16) produces the three main depsides and the three main terpenes, with an accessory compound in *P. orientalis*, which might be diagnostic for this species. Relative abundance of the three main terpenes seems stable within species, but different among species: peltidactylin is the most abundant in *P. occidentalis* and the least abundant in *P. esslingeri* and *P. orientalis*.

The *scabrosella* subclade (Fig. 16) is characterised by the presence of zeorin in large quantity, the other two main terpenes being absent or present in small quantities. With the data currently available, the accessory compounds seem to be diagnostic for each species and for the entire subclade.

The *melanorrhiza* subclade (Fig. 16) has three different chemotypes corresponding to the three species. One accessory compound might be diagnostic for *P. chabanenkoae* and *P. nigriventris*.

The *scabrosa* subclade (Fig. 17) is diverse with *P. borealis and P. neopolydactyla* producing only zeorin and lacking dolichorrhizin and peltidactylin, whereas *P. scabrosa* lacks zeorin. *Peltigera holtanhartwigii* and *P. rangiferina* share an accessory compound, and *P. clathrata* produces all three main terpenes, as well as several accessory compounds.

In conclusion, TLC is most useful in the northern latitudes to distinguish species with a neopolydactyla morphotype (*P. neopolydactyla* lacking peltidactylin and dolichorrhizin can be segregated from other species) and the scabrosa morphotype (*P. borealis* lacking peltidactylin and dolichorrhizin, *P. scabrosa* lacking zeorin).

Several species of the polydactyloid clade have been examined by TLC to further document the variation within the section *Polydactylon*. Two species (*P. dolichospora* and *P. oceanica*; Fig. 18) lack the three main depsides (tenuiorin, methylgyrophorate and gyrophoric acid), and *P.* sp. 8 lacks dolichorrhizin (Fig. 18), showing that the occurrence of this compound is not a shared trait throughout the clade.

## SPECIES DESCRIPTIONS

### 1. The *dolichorhiza* group — Fig. 1, 2

***Peltigera dolichorhiza*** (Nyl.) Nyl., Flora 57: 71. 1874 — MycoBank MB 532352

*Basionym*. *Peltigera polydactylon* f. *dolichorhiza* Nyl. 1860, Syn. Meth. Lich. (Parisiis) 1(2): 327. 1860 — MycoBank MB 635932; Fig. 4a, b, 19a–c, 20a.

*Typus*. ‘Nova Granata’ [Colombia], Bogotá, 2600–2700 m, 1860 (?), *Lindig* 2519 p.p., H-Nyl. 3320, lectotype (!), designated by Galloway (1985) and accepted by Vitikainen (1998).

Epitypification with Colombia, Cundinamarca, Chipaque, Vereda Marilandia, vía desde la carretera hacía el Santuario; N04°26' W74°05', 2400 m; Sept. 2011, on mosses, *R. Lücking & B. Moncada* 33660 (UDBC C-0009731 epitype designated here, MBT 10008458, DUKE isoepitype, Fig. 19a). Epitypification is needed as several species, delimited in this paper with DNA-based species delimitation methods, share the same morphotype and chemistry, and no DNA sequence could be obtained from the lectotype. The chosen epitype belongs to the most common species in the biogeographical area where these species thrive and thus confirms most collections identified under this epithet. The epitype was collected in the same country and presumably the same habitat as the original type.

Reference sequence: OM321433.

*Synonym*. *Peltigera meridiana* Gyeln., Magyar Bot. Lapok 26: 47. 1927b — MycoBank MB 399327; Fig. S11.

*Typus*. Brazil, Minas Gerais, Alto do Itaculumi, Ouro Prêto, coll. *Damazio* 951 (holo W) (!, digital image).

*Thallus* small (1–4 cm diam) to large, c. 5–7 cm (up to 11 cm diam) with lobes 0.7–1.2(–1.5) cm across, typically thin and fragile (several populations from South America have more robust thalli). *Upper surface* beige, pale orange to dark brown, or bluish gray when dry to dark blue when wet, rarely maculate (observed only in specimens with bluish gray thallus when dry), usually distinctly undulate with uneven but distinct depressions, smooth, usually shiny; lobe margins flat or slightly revolute. *Vegetative propagules* not seen. *Lower surface* pale orange to brownish near the margins, becoming dark brown to blackish towards the thallus center; veins indistinct at lobe margins, slightly raised towards the thallus center, usually blackish, forming a distinct pattern with large, numerous, usually elliptical, whitish to pale orange interstices, sometimes covered by a network of orange hyphae especially near lobe margins. *Rhizines* scattered or abundant, usually quite long (0.8–1.3 cm), black or almost black, simple or penicillate, rarely fasciculate and forming a fluffy mass, sometimes quite thick at the base (c. 0.3 mm diam). *Apothecia* rare to abundant, finger- or saddle-shaped, 5–7 mm long, disc dark reddish brown with incised-denticulate margins. *Ascospores* fusiform and elongated, usually slightly bent, 5–9-septate, 71–101 × 3.5–5 μm (n = 22). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: many different phylogroups including V, XVa, XIXa–d (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (minor to major), dolichorrhizin (major), zeorin (trace to minor), and accessory 1, 2, 4 and 5 (Fig. 12, S1).

Barcodes — ITS1 (GATGTCT)**GAAGAAT**(TGTATAA) and ITS2 (AGGTT)**GTACAT**(AGAG) (Fig. 9).

**Fig. 19** a–c. *Peltigera dolichorhiza*. a. Epitype from Colombia (*R. Lücking & B. Moncada* 33660, UDBC); b. upper surface of *P. dolichorhiza* from Colombia (*J. Miadlikowska et al.* NN12, DUKE); c. upper surface of *P. dolichorhiza* from Madagascar (*E. Sérusiaux* DNA4055, LG). — d. *Peltigera itatiaiae*. Holotype from Minas Gerais, Brazil (P1561, *J. Miadlikowska et al.* s.n., CGMS 34399).

Ecology — Mostly over mosses on the ground, on trees (trunks and main branches) and rocks in shady and humid conditions in bushes or forests (mostly montane and often including disturbed stands).

Distribution — Central America: Mexico, Guatemala, Costa Rica, Panama, Jamaica, Dominican Republic; South America: Brazil (Minas Gerais), Colombia, Venezuela, Ecuador, incl. Galapagos Is., Bolivia; Africa: Kenya, Rwanda, South Africa, Madagascar, Reunion Island (Indian Ocean); Amsterdam Island (southern part of the Indian Ocean).

*Selected specimens examined*. **Central and South America**. Bolivia, Dept. Santa Cruz, prov. Florida, Parque Nacional Amboro, S18°03' W63°55’, 2330 m, June 2011, Yungas cloud forest, *M. Kukwa* 9740 (UGDA); ibid., Dept. La Paz, Prov. Nor Yungas, near Siniari colony, S16°13' W67°51', 2190 m, May 2011, *M. Kukwa* 9232 (UGDA). – Brazil, Minas Gerais, Itatiaia National Park, S22°22' W44°41', 2400 m, June 2012, subalpine vegetation, over mosses on soil, *J. Miadlikowska et al.* s.n. (CGMS 34504); ibid., S22°22' W44°41', on mosses on top of boulder partially covered by shrubs, *J. Miadlikowska et al.* s.n. (CGMS 34450). – Colombia, Cundinamarca, Choachi, Paramo de Guasca, 3000–3200 m, *R. Lücking & B. Moncada* 33387 (UDBC); ibid., Boyacá Department, Villa de Leyva, road to Iguaque 2 km from entrance to the park, N5°43' W73°29', 3969 ft, June 2012, low Andean forest with farmland, on mosses on rocks on soily cliff about 7 m high along road, *J. Miadlikowska et al.* NN12 (DUKE). – Costa Rica, San Jose, Reserva Forestal Los Santos, Estacion Biologica Cerro de la Muerte, N9°34' W83°45', 3100 m, Mar. 2003, *J. Miadlikowska* s.n. (DUKE). – Ecuador, Galapagos Is., Isabela, Volcan Sierra Negra, S0°51' W91°8', 1020 m, *M.A. Herrera-Campos* 10693 (CDS); Pichincha, Reserva de vida silvestre Pasochoa, sendero Palma de Cera, S0°26' W78°30', Nov. 2013, bosque secundario, al lado del sendero, base de arbol, sobre musgos, *C. Truong* 3941 (DUKE). – Dominican Republic, San Juan, Aguita Fria Cruce hacia Tetero, N19°2' W70°55', 2136 m, July 2017, evergreen cloud forest, *J.A. Mercado-Díaz et al.* 3075 (F). – Guatemala, Dep. de Quetzeltenango, Municipio de Zunil, road to Fuentes Georginas, N14°45' W91°29', 2442 m, May 2004, *T. Sultan Quedensley* 490 (OMA). – Jamaica, Portland Gap, St. Thomas, Jacob’s Ladder trail to Portland Gap, Blue Mountains National Park, N18°3' W76°36', 1660 m, Apr. 2018, mixed montane forest and disturbed areas, with coffee plantations, on rock among mosses, *J.A. Mercado-Díaz* 3377a & *M. Dal Forno* (F). – Mexico, Oaxaca, Guelatao, Carrera 175 to Ixtlan de Juarez, N17°35' W96°27', 2233 m, Jan. 2008, *Barcenas-Pena* 1224, 1225, 1226, 1230, 1231, 1232 (MEXU); ibid., Sierra de Juarez, Mpio de Ixtlan de Juarez, Entrada al pueblo La Luz, N17° W96°23', 2032 m, Feb. 2002, *M.A. Herrera-Campos* 135 (MEXU); ibid., Hidalgo, Parque Nacional El Chico Llano Grande, N20°10' W98°42', 2967 m, Nov. 2010, forest of *Abies* and *Juniperus*, *M.A. Herrera-Campos* 13377, 13382 (MEXU); ibid., Puebla, Sierra Norte de Puebla, N19°57' W97°26', 640 m, Feb. 2002, tropical mesophilous forest with *Cecropia*, *M.A. Herrera-Campos* 142 (MEXU); ibid., Vera Cruz, Sierra de Los Tuxtlas, Volcan San Martin Tuxtla, N18°34' W95°12', 1450 m, Feb. 2003, *M.A. Herrera-Campos* 227 (MEXU); ibid., Estado de Mexico, Mpio. Isidro Fabela, Poblado Las Palomas, N19°34' W99°29', 3381 m, Apr. 2004, forest of *Abies religiosa*, *M.A. Herrera-Campos* 5466 (MEXU). – Panama, prov. Chiriqui, Volcan Baru, N8°48' W82°33', 2550 m, Apr. 1991, *B. Goffinet* 753 (CONN). – Venezuela, Estado Trujillo, Municipio Bocono, Parque Nacional Guaramacal, 369882E 1020890N, Oct. 2006, *N. Cuello* & *W. Albarran* 3162 (B 600164810). – **Africa**. Madagascar, Angavokely Forest Station, S18°56' E47°44', 1770–1780 m, Oct. 2008, degraded montane forest, *E. Sérusiaux* s.n. (LG); ibid., Oct. 2014, *E. Sérusiaux* 4055 (LG). – France, Amsterdam Is., S37°49" E77°34', Dec. 2007, ‘Grand Bois de Phylicas’, sea level, on sand in shade of *Phylica* and *Elaphoglossum*, *B. Van de Vijver* AMS07L28 (BR); La Réunion, Caldera of the volcano La Fournaise, W side at Pas de Bellecombe, S21°13' E55°42', 2230–2240 m, May 2008, basaltic cliff in fresh and mossy conditions, *E. Sérusiaux* s.n. (LG, REU); ibid., W of ‘Plaine d’Affouches’, track towards ‘Piton des Fougères’, S20°58' E55°24', 1400–1500 m, Nov. 2009, *Erica*-thickets, *N. Magain* & *E. Sérusiaux* s.n. (LG). – Kenya, Mt Kenya National Park, S00°09' E37°26', c. 3030 m, Sept. 2002, montane forest with *Hagenia abyssina* and *Juniperus procera* with swamps dominated by *Carex kenyensis*, *E. Fischer* & *D. Killmann* s.n. (KOBL, LG); ibid., Central Province, Nyeri District, Aberdare National Park, Aug. 1985, *K. Kalb* 13931 (DUKE). – Rwanda, Volcanoes National Park, Karisoke, S01°29' E29°29', c. 3200 m, Oct. 2010, montane forest with *Hagenia abyssinica* and *Hypericum revolutum*, *E. Sérusiaux* s.n. (LG). – South Africa, Western Cape Province, Vicinity of Knysna, Diepwalle forest, Ysterhoutrug, S33°58' E23°9', 443 m, Oct. 2010, *B. Goffinet* 10299 (CONN); ibid., Cape Town, Table Mountain National Park, Skeleton Gorge trail, S33°59' E18°25', June 2019, on mosses on rocks along trail, 20 m from creek, *F. Lutzoni* FL23 (DUKE).

Notes — *Peltigera dolichorhiza* is a widely used name applied to any tropical population with a thin and fragile thallus, smooth, usually uneven upper surface with distinct depressions, raised-digitate apothecia, pale lower surface near margins, distinct network of white elliptical interstices over fused, flat, dark, rather indistinct veins (near thallus center), simple and long rhizines, and the presence of several triterpenoids including at least one of these three: dolichorrhizin, peltidactylin or zeorin (Swinscow & Krog 1988, Galloway 2007). As thus circumscribed, the species was considered to be pantropical and also to occur in temperate areas of the southern hemisphere (Swinscow & Krog 1988, Galloway 2000, 2007). More recently it was suggested (Sérusiaux et al. 2009) and demonstrated (Magain et al. 2017a, b) that *P. dolichorhiza* represents a species complex. Molecular inferences and species delimitation methods grouped widespread populations of the typical dolichorhiza morphotype, including material from South America (e.g., Colombia), the Galapagos archipelago and tropical Africa, within a single lineage that can be assigned to *P. dolichorhiza* s.str. To avoid any ambiguity, we epitypified *P. dolichorhiza* with a recent collection from the same country (see § Nomenclature and typification of validly published epithets).

*Peltigera meridiana* was first introduced as a nom. nud. (Gyelnik 1927a), then formally described (Gyelnik 1927b), subsequently reduced to a variety of *P. nana* (Gyelnik 1932, 1936, Vitikainen 1998). The scientific legacy of Gyelnik is controversial as he introduced many new epithets in the Peltigerales on the basis of poor material and usually erroneous observations. Vitikainen (1994b, 1998), however, spent considerable time assessing the taxonomic validity of many of Gyelnik’s epithets in *Peltigera*, suggesting that *P. meridiana* could be synonymised within *P. dolichorhiza*. Based on the detailed photographs of *P. meridiana* material collected in Brazil provided by the curator of the Vienna Herbarium (W), we can attest that the type specimen of *P. meridiana* represents the dolichorhiza morphotype. Therefore, we consider it is a synonym of *P. dolichorhiza*, the most common species with that morphotype in South America, including in Minas Gerais (Brazil) where the type of *P. meridiana* was collected.

Typically, *P. dolichorhiza* is thin and brittle and has a pale orange lower surface (near lobe margins) with a network of flat, blackish veins and whitish interstices, especially towards the thallus center; rhizines are black, long and simple. However, Neotropical populations of *P. dolichorhiza* s.str. can also develop rather thick and robust thalli, and/or penicillate or fasciculate rhizines sometimes forming fluffy mass covering the lower surface of the thallus. In South America (e.g., Minas Gerais region of SE Brazil), ITS barcodes are necessary for reliably distinguishing *P. dolichorhiza* s.str. from the other newly recognised species from the *dolichorhiza* group: *P. itatiaiae*, *P. massonii* and *P. kukwae*, although well-developed populations can also be recognised based on morphology.

*Peltigera kukwae* var. *kukwae* has two morphotypes: one with rather robust, dark brown, almost flat thallus (with depressions hardly visible), and another one resembling typical dolichorhiza morphotype. However, in both morphotypes the veins are rather sparse and therefore the interstices relatively large (2.5–4 × 2–3 mm), a feature rarely seen in other species.

*Peltigera massonii* is characterised by its rather dark brown and typically shiny thallus and lower surface with flat, fused, black veins, leaving almost no interstices (stanleyensis morphotype).

*Peltigera itatiaiae* tends to have a lower surface somewhat typical of the hymenina morphotype (veins flat and poorly delimited, forming a rather dense network towards margins with hardly visible interstices), differing however, by its abundant, relatively long rhizines (0.8–1 cm), which are dark brown to black, fas-

**Fig. 20** Pictures of *Peltigera* species in the field in Colombia. a. Epitype of *Peltigera dolichorhiza*; b. *Peltigera massonii*; c, d. *Peltigera kukwae* var. *phyllidiata*.

ciculate to brush-like or fibrillose, and which sometimes form dense mats towards the thallus center.

Most specimens of *P. dolichorhiza* s.str. are usually correctly identified, though many collections from tropical areas, especially in South America were named as *P. neopolydactyla* or *P. polydactylon*, but neither occurs on this continent.

At the exception of *P. seneca* that was recently found on Mt Kilimandjaro (Kaasalainen 2022), all collections available from tropical Africa (incl. Madagascar and the Mascarene archipelago) of section *Polydactylon* represent *P. dolichorhiza* s.str.; they most probably originated from a single and recent colonizing event from South America because they all share the same two haplotypes, which differ by a single indel in the ITS1 region and were also found in Brazil/Minas Gerais. The record of *P. dolichorhiza* from Amsterdam Island in the southern part of the Indian Ocean (c. S37°49' E77°34'; Nylander 1886, Aptroot et al. 2011) was confirmed, thus representing the most eastern and perhaps the most southern locality for this species. The only additional species from the *dolichorhiza* group which occurs outside South America is *P. truculenta* (see description of this species below).

Populations from Papua New Guinea reported by Sérusiaux et al. (2009) correspond to the following species: *P. dolichorhiza* s.lat. A represents an undescribed species in the *hymenina* group, *P. dolichorhiza* s.lat. B represents *P. stanleyensis*, *P. dolichorhiza* s.lat. C represents *P. elixii* and *P. dolichorhiza* s.lat. D represents *P. serusiauxii* from the polydactyloid clade (Magain et al. 2020; *P.* sp. 11 in Magain et al. 2017a, b).

No material was available from the Indian subcontinent and from most of the Indo-Malay biogeographical realm (Olson et al. 2001) and therefore we could not verify the existing records of *P. dolichorhiza* from this large and diverse zone (Awasthi & Joshi 1982). However, based on the revised circumscription of this species, its presence in these regions is unlikely.

***Peltigera itatiaiae*** Magain, Miadl. & Sérus., *sp. nov.* — MycoBank MB 845021; Fig. 19d

*Synonym*. *Peltigera* sp. 2B in Magain et al. (2017b).

*Etymology*. Named for Itatiaia National Park, Brazil, created in 1937 and home to Mata Atlântica, one of the most threatened forest habitats on the planet.

*Typus*. Brazil, Minas Gerais, Itamonte, Itatiaia National Park, S22°22' W44°45', 1810 m, June 2012, atlantic rain forest, very wet mossy slope, *J. Miadlikowska et al.* s.n. (holo CGMS 34399).

Reference sequence: KX897341.

*Thallus* large (c. 7–10 cm across) with lobes 0.8–1.4 cm across, thin and fragile, especially towards flat or slightly raised lobe margins, which become very brittle. *Upper surface* pale bluish gray becoming darker bluish when wet, distinctly undulating with uneven depressions, smooth, matt or slightly shiny. *Vegetative propagules* not seen. *Lower surface* whitish to pale orange near the lobe margins, becoming darker towards the thallus center; veins broad, flat or slightly raised and poorly delimited, forming a rather dense network towards the lobe margins where interstices are poorly visible, in contrast with better defined, numerous whitish, oval or irregular shape (up to 2–3.5 mm in length) interstices towards the thallus center. *Rhizines* abundant, scattered near the lobe margins but sometimes forming dense mats towards the thallus center, quite long (0.8–1 cm), dark brown to black, fasciculate to brush-like, becoming fibrillose. *Apothecia* and *pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: V, XIX (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (minor), dolichorrhizin (major), zeorin (trace), and accessory 2 and 5 (Fig. 12, S1).

Barcodes — ITS1 (AAAGC)**TGTAGGA**(TAAAAAA) (Fig. 9).

Ecology — On rocky cliffs in very humid sites in forests.

Distribution — Endemic to SE Brazil, the Mata Atlântica biome; all collections are from Itatiaia National Park.

*Selected specimens examined*. Brazil, Minas Gerais, Itamonte, Itatiaia National Park, S22°23' W44°45', 2350 m, June 2012, atlantic rain forest, on rocky cliff (very humid site), *J. Miadlikowska et al.* s.n. (CGMS 34562); ibid., S22°23' W44°44', 1830 m, June 2012, atlantic rain forest, *J. Miadlikowska et al.* s.n. (CGMS 34428).

Notes — *Peltigera itatiaiae* is closely related to other species with typical dolichorhiza morphotype and it is largely sympatric with *P. dolichorhiza* and *P. kukwae* var. *kukwae* (Fig. 1). ITS is needed for accurate identification of this species. For morphological differences see notes under *P. dolichorhiza*. *Peltigera* sp. 2ab, another potentially new species within this complex with morphology somewhat intermediate between *P. itatiaiae* and *P. massonii* (Magain et al. 2017b) lacks strong support to be separated from *P. itatiaiae* and *P. massonii*, and it is too poorly sampled to be formally introduced. Both *Nostoc* phylogroups associated with *P. itatiaiae* are shared with *P. dolichorhiza* s.str.

### ***Peltigera kukwae*** Magain, Miadl. & Sérus., *sp. nov*. — MycoBank MB 845022; Fig. 21a

*Synonym*. *Peltigera* sp. 1 (assigned to var. *phyllidiata*: see below), *P. dolichorhiza* 2 in Magain et al. (2017b), *P. dolichorhiza* 3.

*Etymology.* This new species is dedicated to Martin Kukwa, an accomplished systematist and a friend from Poland, for his contributions to lichen biodiversity research in South America, including an assessment of Peltigerales in Bolivia (Kukwa et al. 2014).

*Typus*. Brazil, Minais Gerais, Itatiaia National Park, S22°22' W44°43', 2347 m, June 2012, rocky cliff, *J. Miadlikowska et al.* s.n. (holo CGMS 34530).

Reference sequence: KX897188.

*Thallus* large (c. 5–8 cm across) with lobes 0.7–1.0 cm wide, of two different morphotypes: thin and fragile with the upper surface bluish gray when dry to dark blue when wet, or rather robust with the upper surface dark brown when dry to darker when wet. *Upper surface* distinctly undulating with uneven but distinct depressions, sometimes depressions indistinct and thallus smooth, matt or shiny; margins flat, rarely slightly raised or slightly revolute. *Vegetative propagules* not seen. *Lower surface* pale orange to brownish near the margins; veins distinct or not well visible at the lobe margins, becoming slightly raised and blackish towards the thallus center forming a distinct network of rather large, elliptical interstices (2.5–4 × 2–3 mm). *Rhizines* scattered or abundant, covering almost the entire lower surface and thus without any interstices visible, usually quite long (0.5–0.9 cm), black or almost black, simple, rarely fasciculate, sometimes quite thick at the base (0.2 mm diam). *Apothecia* rare, saddle-shaped, 5–7 mm long, disc dark reddish brown with incised-denticulate margins. *Ascospores* fusiform and elongated, usually slightly bent, 5–7(–9)-septate, 74–98 × 3.5–5 µm (n = 22). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: XIX, XIXc, XIXd (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (major), dolichorrhizin (major), zeorin absent or trace, and accessory 1 and 2 (Fig. 12, S1).

Barcode for *Peltigera kukwae* var. *kukwae* — ITS1 (GGG) **ATAAAAAAGACTATGAAA**(CCTATGA) (Fig. 9); *P. kukwae* var. *phyllidiata* has a different barcode (see below).

Ecology — On mossy rock cliffs in very humid sites, or over mosses on dead trunks.

Distribution — Ecuador, Brazil/Minas Gerais.

*Selected specimens examined*. Brazil, Minais Gerais, Itatiaia National Park, S22°22' W44°45', c. 1800 m, June 2012, *J. Miadlikowska et al.* s.n. (CGMS 34408). – Ecuador, Napo, Volcan Sumaco, S0°33' W77°37', 3000 m, 'arriba de cabaña 3, Ceja andina', mosses on dead trunk, *C. Truong* 3979 (DUKE).

Notes — In previous studies, this species was referred to as *P.* sp. 1, *P. dolichorhiza* 2 and *P. dolichorhiza* 3, which were delimited as distinct species or not depending on the priors applied to species delimitation analyses (Magain et al. 2017b). It can be distinguished from other morphologically similar and co-occurring species (*P. dolichorhiza*, *P. itatiaiae* and *P. massonii*) by its rather large interstices (2.5–4 × 2–3 mm) on the lower side; however, the barcode (ITS) sequence is needed for its reliable identification; see notes under *P. dolichorhiza*. The two *Nostoc* phylogroups that *P. kukwae* var. *kukwae* associates with were also found with *P. dolichorhiza* (Magain et al. 2017a).

### ***Peltigera kukwae*** var. ***phyllidiata*** Magain, Miadl. & Sérus., *var. nov*. — MycoBank MB 8450213; Fig. 20c, d, 21b, c

*Synonym*. *Peltigera* sp. 1 in Magain et al. (2017b).

*Etymology*. The epithet refers to the presence of phyllidia, otherwise unknown in section *Polydactylon* in the Neotropics.

*Typus*. Bolivia, Dept. La Paz, Prov. Nor Yungas, near Chuspipata village, S17°17' W67°51', 3228 m, May 2011, cloud forest with *Ericaceae*, *M. Kukwa* 9276 (holo LPB; iso UGDA).

Reference sequence: KX897335.

*Thallus* c. 5–8 cm across forming irregular patches, with elongate lobes, less than 0.5 cm wide, thin and very brittle when dry; hirsute and ovoid aborted primordia of apothecia sometimes frequent along lobe margins. *Upper surface* undulating, typically not scrobiculate, smooth and glossy with margins typically raised and rather crisped; bluish gray to greenish brown to brownish when dry, becoming darker when wet. *Phyllidia* usually present along lobe margins, rounded to dissected, rarely digitate, less than 2 mm long, brittle and easily broken off; when phyllidia absent, the lobe margins are nevertheless irregularly dissected, with parts of the lobes erect and slightly wrapped. *Lower surface* cream-colored to orange-brown; veins flat or almost flat, pale orange to dark brown towards the thallus center, diffused and not forming a clear pattern, but when dark, a branched and anastomosing pattern can be observed, especially in contrast with the pale orange interstices. *Rhizines* abundant and conspicuous, up to 0.5–0.7 cm long, dark brown to black, simple to fasciculate. *Apothecia* and *pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: XIX, XIXc (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (minor), dolichorrhizin (major), zeorin hardly detected or absent, and accessory 1 and 2 (Fig. 12, S1).

Barcodes — ITS2 (TCATA)**GGAATTT**(CGGTATT) (Fig. 9).

Ecology — On soil and mossy tree trunks and branches in humid montane forests; at 3200–3500 m elevation.

Distribution — Colombia and Bolivia but expected to occur elsewhere in the tropical mountains of South America.

**Fig. 21** a. Holotype of *Peltigera kukwae* var. *kukwae* from Minas Gerais, Brazil (P1567, *J. Miadlikowska et al.* s.n.; CGMS 34530); b, c. *Peltigera kukwae* var. *phyllidiata*, b. holotype from Bolivia (B, *M. Kukwa* 9276, LPB), c. specimen from Colombia (C, *R. Lücking & B. Moncada* 33334, UDBC). — d. *Peltigera massonii*. Holotype from Ecuador (*D. Masson* EC003, QCNE).

*Selected specimens examined*. Bolivia, Dept. La Paz, Prov. Nor Yungas, near Chuspipata village, S17°17' W67°51', 3228 m, May 2011, cloud forest with *Ericaceae*, *M. Kukwa* 9327 (UGDA, DUKE; mentioned under *P. polydactylon* in Kukwa et al. 2014); ibid., Parque Nacional y Area Natural de Manejo Integrado Cotapata, S16°17' W67°53', 3520 m, May 2011, transition Páramo Yungeño-Yungas montane cloud forest, *M. Kukwa* 9440 (UGDA, DUKE; mentioned under *P. polydactylon* in Kukwa et al. 2014). – Colombia, Cundinamarca, Mun. Guasca, Páramo de Guasca, 3200 m, *R. Lücking & B. Moncada* 33334, 33339 (UDBC); ibid., Páramo El verjón, Parque Ecológico Matarredonda, Bogota-Choachí road, N4°34' W74°, on mosses below small shrubs in a low altitude paramo, *C.J. Pardo-De la Hoz* 798 (ANDES).

Notes — Within section *Polydactylon*, *P. kukwae* var. *phyllidiata* differs from the known South American *Peltigera* by its slightly narrower lobes, dissected lobe margins decorated most of the time with marginal phyllidia. Other phyllidiate species in South America include: a) *P. andensis* (Vitikainen 1995) from section *Horizontales*, which has a lower surface with mostly indistinct veins and produces flat, rounded or oval apothecia (rare); b) *P. austroamericana* and *P. fibrilloides*, which form a species complex in section *Peltigera* (Magain et al. 2018) without any detectable lichen substances (Vitikainen 2004); and c) *P. friesiorum* from section *Peltigera* (Vitikainen 1998, Magain et al. 2018), which has a tomentose upper surface. *Peltigera kukwae* var. *phyllidiata* was previously reported from Bolivia under *P. polydactylon* (Kukwa et al. 2014), but no members of the polydactyloid clade are known to occur in South America. If all collections included in Kukwa et al. (2014) under *P. polydactylon* belongs to *P. kukwae var. phyllidiata*, the altitudinal range of this taxon in Bolivia is 2570–3520 m. Infraspecific level was chosen for this taxon because it appears nested within the diversity of *P. kukwae* (Fig. 2).

### ***Peltigera massonii*** Magain, Miadl. & Sérus., *sp. nov*. — MycoBank MB 845024; Fig. 20b, 21d, 22a

*Synonym*. *Peltigera* sp. 2 in Magain et al. (2017b).

*Etymology*. This new species is dedicated to our distinguished colleague and friend, Didier Masson, for his several important contributions to lichen biodiversity. He also collected the type material.

*Typus*. Ecuador, Pichincha prov., Yanacocha Reserve, S0°07' W78°25', 3545 m, July 2016, on the ground along track in 'Bosque siempreverde montano alto', *D. Masson* EC003, LG DNA 6187 (holo QCNE; iso LG, hb Masson).

Reference sequence: MT488056.

*Thallus* large (c. 5–8 cm across) with lobes 0.7–1.4 cm across; thin and fragile. *Upper surface* distinctly undulating with uneven depressions, smooth, usually shiny, lobe margins flat or slightly revolute; grayish brown to usually dark brown, bluish gray when wet. *Vegetative propagules* not seen. *Lower surface* pale orange near lobe margins; veins broad, flat and diffuse (poorly delimited), soon becoming dark brown to black, fused and covering the entire surface leaving a few whitish, oval to irregular interstices 1–2 × < 1 mm in size. *Rhizines* scattered to abundant, quite long (0.8–1 cm), black or almost black, simple or fasciculate. *Apothecia* rare, saddle-shaped, 3–4 mm long, disc reddish brown with incised-denticulate margins. Mature *ascospores* not seen. *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: XVa, XIX (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major to minor) and gyrophoric acid (trace); triterpenes: peltidactylin (major), dolichorrhizin (major), zeorin (trace), and accessory 1–6 present in significant quantities (Fig. 12, S2).

Barcodes — ITS2 (TTGG)**CAAGAATGCTG**(TTCTA) (Fig. 9).

Ecology — On slopes, rocks or rocky cliffs in humid conditions in montane forests and paramos at 2500–3500 m elev. in the Andes, and high elevations in SE Brazil in the Mata Atlântica biome.

Distribution — Brazil/Minas Gerais, Colombia and Ecuador.

*Selected specimens examined*. Brazil, Minas Gerais, Itamonte, Itatiaia National Park, S22°22' W44°43', 2345 m, June 2012, on rocky cliff (very humid site), *J. Miadlikowska et al.* s.n. (CGMS 34526, 34544). – Colombia, Cundinamarca, Choachi, Paramo de Guasca, 3000–3200 m, *R. Lücking & B. Moncada* 33361 (UDBC); ibid., Cauca, Purace, Mina de Azufre, N2°22' W76°25', 3200–3500 m, May 2012, on rocks (*Ericaceae* belt), *D. Diaz Escandon et al.* s.n. (ANDES, DUKE); Cocora, Quindío, Los Nevados National Park, trail to 'Estrella de Agua', 400 m upstream from N4°38' W75°28', 2560 m, May 2012, 'High Andean' forest, very dense except along the trail, very humid and shady, on boulder covered with mosses, *F. Lutzoni* & *J. Miadlikowska* 77 (with *L. Coca*) (ANDES).

Notes — *Peltigera massonii* displays the stanleyensis morphotype, with its brown shiny slightly undulating upper surface. Unlike *P. stanleyensis* which displays the same morphotype, its lower surface has a few interstices (whitish, oval to irregular interstices 1–2 × < 1 mm in size). *Peltigera massonii* is largely sympatric with *P. dolichorhiza*, *P. itatiaiae* and *P. kukwae* (see discussion under each species); ITS is needed for their accurate separation. Both *Nostoc* phylogroups found in *P. massonii* are shared with three other rather common species from the *dolichorhiza* group in South America: *P. dolichorhiza*, *P. pulverulenta* and *P. truculenta* (Magain et al. 2017a).

### ***Peltigera pulverulenta*** (Taylor) Nyl., Acta Soc. Sci. Fenn. 7: 435. 1863 — MycoBank MB 399351; Fig. 22b–d, 23a, b, 24a, b

*Basionym*. *Peltidea pulverulenta* Taylor, London J. Bot. 6: 184. 1847 — MB 399263

*Synonym*. *Peltigera pulverulenta* 1 in Magain et al. (2017b).

*Typus*. Ecuador, 'Pillzhum, Prof. *W. Jameson*', lectotype FH (!); isolectotype H-Nyl 33106 (!) (Vitikainen 1998: 136).

https://plants.jstor.org/stable/10.5555/al.ap.specimen.h9506053.
https://plants.jstor.org/stable/10.5555/al.ap.specimen.g00293091.

Epitypification with Ecuador, Napo, Volcan Sumaco, arriba de cabaña 3, camino al crater, S0°33' W77°38', 3300 m, Nov. 2013, mosses on dead trunks, *C. Truong* 3982 (QCNE, epitype designated here, MBT 10008459, DUKE, isoepitype). Epitypification is needed as several species, delimited in this paper with DNA-based species delimitation methods, share the same morphotype and chemistry, and no good quality DNA could be obtained from the lectotype. The chosen epitype belongs to the most common species in the biogeographical area where these species thrive and thus confirm most collections identified under this epithet. The epitype was collected in the same country and presumably the same habitat as the original type.

Reference sequence: OM349079.

*Synonym*. *Peltigera microdactyla* Nyl., Ann. Sci. Nat. Bot., Sér. 5, 7: 304. 1867 — MycoBank MB 399329.

*Typus*. Venezuela, 'Merida, Colonia Tovar' [= 'Aragua, Tovar' fide Vitikainen 1998: 137], coll. *Moritz*, holotype H-Nyl 33100 (!) (Vitikainen 1998: 137).

https://plants.jstor.org/stable/10.5555/al.ap.specimen.h9506054.

*Thallus* forming rounded rosettes up to 9–10 cm diam. In well-developed populations, but often divided into parts consisting of a few lobes or a single one, lobes usually elongated to sometimes almost rounded; populations with smaller thalli (c. 3–5 cm diam) have usually rounded (up to 0.4–5 mm wide), sometimes overlapping lobes, rather thick and spongy, sometimes thinner but not fragile or papery. *Upper surface* typically scabrous, with plane or almost plane lobe margins; brownish to dark brown or much paler to pale grey or bluish gray, sometimes polychromatic. *Vegetative propagules* absent, or developed as small marginal granules, which sometimes become rather large and abundant. *Lower surface* whitish to ochraceous-creamy; veins almost flat to raised, sometimes forming a large and dense hirsute layer that becomes dark brown to almost black, especially in thalli with a dark brown upper surface; interstices elongated

**Fig. 22** a. *Peltigera massonii* from Brazil (*J. Miadlikowska et al.* s.n., CGMS 34544). — b–d. *Peltigera pulverulenta*. b. Epitype from Ecuador (*C. Truong* 3982, QCNE); c, d. from Colombia (*D. Fonseca* & *F. Martinez* 214, UDBC), c. upper and d. lower surface.

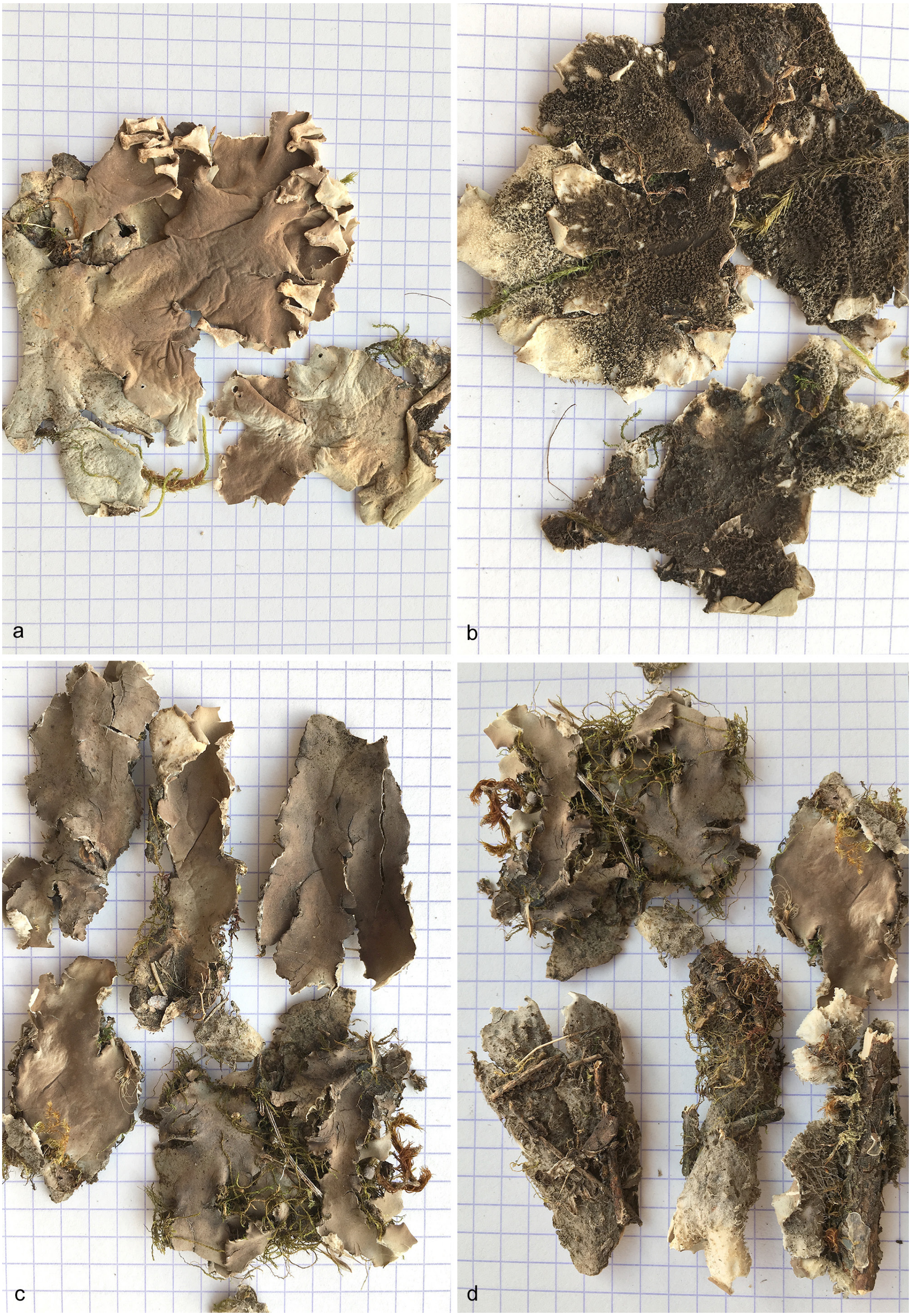

**Fig. 23** a, b. *Peltigera pulverulenta* from Bolivia (*M. Kukwa* 9552, UGDA), a. upper and b. lower surface. — c, d. *Peltigera sipmanii* holotype from Ecuador (*C. Truong* 3942, QCNE), c. upper and d. lower surface.

**Fig. 24** Pictures of selected *Peltigera* species in the field in Colombia. a, b. *Peltigera pulverulenta*; c, d. *Peltigera willdenowii.*

or ovoid, whitish, sometimes sparse when veins are fused and covered with rhizines. *Rhizines* abundant, pale to almost white to black, sometimes forming dense mats that covers the lower surface, very short near lobe margins but becoming quite long towards thallus center, predominantly fibrillose. *Apothecia* rare, saddle-shaped, 4–6 mm long, disc dark brown to reddish brown, typically denticulate. Excipulum outer surface rugose. *Ascospores* filiform and flexuose, almost cylindrical and becoming thinner towards the ends, (5–)7(–9)-septate, 94–109 × 3–4 µm (n = 19). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: XVa, XIX, XIXb (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (major to minor), dolichorrhizin (major), zeorin (minor to trace), and accessory 2 and 5 (Fig. 13, S2).

Barcodes — ITS1 (CACACA)**TAAAGCA**(TTGAGTT) and ITS2 (GGTTGT)**CATAAGAA** and ITS2 (GGTAA)**TAATGCTG** (TTC)**AAAAACCAG**(TCAAAAA) (Fig. 9).

Ecology — On rocks, mossy ground or branches in humid high-altitude forests.

Distribution — Mexico/Oaxaca, Ecuador, Colombia, Venezuela, Brazil/Minas Gerais, Bolivia.

*Selected specimens examined.* Bolivia, Dept. La Paz, Prov. Murillo, Valle del Zongo, páramo Yungeño, S16°10' W68°08', 3375 m, May 2011, *M. Kukwa* 9552 'ex-UGDA-L-17721' (UGDA); ibid., Prov. Larecaja, Jocollone village, S15°38' W68°41', 3545 m, May 2011, páramo Yungeño vegetation, open anthropogenic area, *M. Kukwa* 8536 'ex-UGDA-L-17702' (UGDA). – Brazil, Minais Gerais, Itatiaia National Park, Itamonte, S22°22' W44°43', 2345 m, June 2012, rocky cliff along road, very humid site, *J. Miadlikowska et al.* s.n. (CGMS 34548); ibid., S22°22' W44°44', 1830 m, June 2012, rocky cliff along road, very humid site, *J. Miadlikowska et al.* s.n. (CGMS 34445, 34566). – Colombia, Cundinamarca, Choachi, Paramo de Guasca, 3000–3200 m, *R. Lücking & B. Moncada* 33301, 33328, 33383 (UDBC); ibid., Páramo El verjón, Parque Ecológico Matarredonda, Bogota-Choachí road, growing on *Chusquea* in low altitude paramo, *C.J. Pardo-De la Hoz* 920 (ANDES); ibid., Cauca, Purace, Mina de Azufre, N2°22' W76°25', 3200–3500 m, May 2012, on rocks (*Ericaceae* belt), *D. Diaz Escandon et al.* s.n. (ANDES); ibid., Dep. De Boyacá, Municipio El Cocuy, Parque Nacional Natural El Cocuy, Alto de la Cueva, 3800 m, *D. Fonseca* & *F. Martinez* 214 (UDBC). – Ecuador, Pichincha, Reserva de vida silvestre Pasochoa, sendero Los Pantzas, en la cumbre, S0°26' W78°29', 3547 m, *C. Truong* 3945 (DUKE). – Mexico, Oaxaca, Sierra de Juarez Ixtlan de Juarez, N17°23' W96°27', 3341 m, Jan. 2002, *M.A. Herrera-Campos* 122 (MEXU).

Notes — In montane biomes of Central and South America, *P. pulverulenta* and two additional lineages recognised as putative species in Magain et al. (2017a) (*P. pulverulenta* 2 and 3) form a strongly supported clade. They typically develop the pulverulenta morphotype and have no diagnostic morphological or chemical characters to distinguish among them. The most common and widespread are populations representing *P. pulverulenta* 1 (Magain et al. 2017a), which also includes morphs with smaller, thinner thalli and distinct venation pattern recognised as *P. microdactyla* (Vitikainen 1998). To avoid any ambiguity, we epitypified *P. pulverulenta* (corresponding to *P. pulverulenta* 1 lineage), which as such represents the most common species with a pulverulenta morphotype in the Neotropics, and we further reduce *P. microdactyla* into synonymy with it.

*Peltigera pulverulenta* associates with several *Nostoc* phylogroups, all of which are shared with several species from the *P. dolichorhiza* group (Magain et al. 2017a). Specimens with the pulverulenta morphotype from southern Chile and Gough Island belong to *P. truculenta* var. *austroscabrosa*.

***Peltigera sipmanii*** Magain, Miadl. & Sérus., *sp. nov*. — MycoBank MB 845025; Fig. 23c, d

*Synonym*. *Peltigera pulverulenta* 3 in Magain et al. (2017b).

*Etymology*. The species name honours our distinguished colleague and friend Harrie J.M. Sipman for his important contributions to lichen diversity research in Central and South America.

*Typus*. Ecuador, Pichincha, Reserva de vida silvestre Pasochoa, sendero Los Pantzas, en la cumbre, S0°26' W78°29', 3547 m, Sept. 2013, *C. Truong* 3942 (holo QCNE; iso DUKE).

Reference sequence: MT488050.

Morphologically similar to *P. pulverulenta* (see description of this species).

Diagnosis – *Peltigera sipmanii* is recognised by its barcode in ITS1, a 6-nucleotide motif AGAAAA located 170 bp after the start of ITS1 between motives TTGCCC and CTACCT.

Photobiont — Unique haplotype HT34 based on a single record (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (major), dolichorrhizin (major), zeorin (trace), and accessory 1, 2 and perhaps 5 (Fig. 13, S2).

Barcodes — ITS1 (TTGCCC)**AGAAAA**(CTACCT) (Fig. 9).

Ecology — On mossy ground, rocks, branches in humid high altitude forests.

Distribution — Ecuador, Colombia, Costa Rica.

*Selected specimens examined*. Colombia, Departamento de Boyacá, Municipio El Cocuy, Parque Nacional Natural El Cocuy, Alto de la Cueva, 3800 m, *D. Fonseca* & *F. Martinez* 199 (UDBC); ibid., Cundinamarca, La Calera, Parque Chingaza, Piedras Gordas, Sector Lagunas, 3300–3600 m, *R. Lücking & B. Moncada* 34033 (UDBC); ibid., Páramo El verjón, Parque Ecológico Matarredonda, Bogota-Choachí road, N4°34' W73°58', on rocks by a stream and surrounded by mosses (high andean rain forest/lower paramo), *C.J. Pardo-De la Hoz* 743 (ANDES). – Costa Rica, San Jose, Reserva Forestal Los Santos, Estacion Biologica Cerro de la Muerte, N9°34' W83°45', 3100 m, Mar. 2003, *J. Miadlikowska* DNA-P37 (DUKE).

Notes — No morphological or chemical characters distinguish *P. sipmanii* from its relatives with the pulverulenta morphotype. The ITS barcode is needed for a valid identification of this species.

***Peltigera truculenta*** De Not., Osservazioni sulla tribù delle Peltigeree, Mem. Reale Accad. Sci. Torino ser. 2, 12: 134. 1851 — MycoBank MB 399372; Fig. 25a, b

*Typus*. Chile, Valparaiso, 1847, Puccio, comm. De Negri, (location of type unknown; M, isotype, fide Vitikainen 2002, (! digital image)).

Reference sequence: KX897399.

https://plants.jstor.org/stable/10.5555/al.ap.specimen.m0012399.

*Synonym*. *Peltigera chilensis* Gyeln., Bryologist 34: 17. 1931. — MycoBank MB 399289.

*Typus*. Chile, Los Lagos, Panguipulli, 'an alten Bäumen, morschem Holze im Walde', Höhe ü. D. M 200 m', *Hollermayer* 664 (holo B, destroyed; iso BP not found).

*Thallus* forming rounded patches, ranging from small (2–3 cm diam) with rather raised and narrow lobes to large (8–10 cm diam) with broad lobes up to 0.8–1 cm wide, thin and papery and thus fragile or more coriaceous and then not brittle. *Upper surface* slightly undulating to slightly scrobiculate, smooth and shiny mostly at lobe tips, rarely matt; lobe margins plane to involute, raised if thalli small; light greenish gray or bluish gray to gray brown or dark brown, becoming darker when wet. *Vegetative propagules* absent. *Lower surface* pale in the interstices, ranging from whitish to pale brown; veins almost flat, poorly delimited, becoming wider and fused towards the thallus center where the interstices are not visible, ochraceous at lobe margins and soon becoming brown to black towards the thallus center. *Rhizines* few or rarely abundant, up to 1 cm long, dark brown to black, simple to fasciculate, rarely branched. *Apothecia* often absent, if present, usually abundant, saddle-shaped, 0.4–0.5 cm long, disc reddish brown to dark brown, with a crenate margin when young. *Ascospores* fusiform and elongated, sometimes bent or flexuose, 5–7-septate, 72–94 × 3.5–4.5 µm (n = 18). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: VIIIb, XVb (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major to trace) and gyrophoric acid (trace); triterpenes: peltidactylin (major to minor), dolichorrhizin (major to minor), zeorin not detected, and accessory 4 and 7 (Fig. 13, S3).

Barcodes — ITS1 (GTCTG)**AACGA**(TTGTAT) and ITS2 (TTGTCA)**TACGAAT**(TCGGTA) (Fig. 9). These barcodes distinguish *P. truculenta* at the species level, including the two varieties.

Ecology — Ubiquitous species, growing on a broad range of substrates, including, bark, mosses on bark, and the forest floor, frequent on soil; always at low altitudes.

Distribution — South America: Chile, from Valvidia to Cape Horn, Argentina/Tierra del Fuego; Gough Island in the southern Atlantic Ocean and also reported from two subantarctic islands (Crozet and Kerguelen Islands).

*Selected specimens examined*. Argentina, Tierra del Fuego, Isla Grande, Bahia Brown, 20 m, lowland forest of *Nothofagus punilio*, on soil, *S. Stenroos* 2377 (H); ibid., prov. Rio Negro, Parque Nacional Nahuel Huapi, on trail Puerto Blest to Lago Los Cantaros, S41°01' W71°49', 770 m, Dec. 1999, humid *Nothofagus dombeyi* forest, *O. Vitikainen* 16275 (H). – Chile, Reserve Nacional Rio Simpson, S45°29' W72°15', 178 m, Jan. 2008, on mineral soil in closed, young *Nothofagus* forest, *T. Wheeler* & *P. Nelson* 6156 (CONC); ibid., Antarctica Chileana Prov., comuna de Cabos de Hornos, Isla Navarino, S54°56' S67°39', ± sea level, Jan. 2011, along trail through mixed *Nothofagus forest*, *B. Goffinet* 10433, 10438, 10440 (CONN); ibid., Parque Etnobotánico Omora, c. 3 km W of Puerto Williams, between S54°57' W67°38' and S54°58' W67°38', 100–650 m, Jan. 2015, along trail from Robalo waterfall to alpine vegetation at Cerro LaBandera through mixed *Nothofagus* forest to above tree-line, *B. Goffinet* 12912 (CONN); ibid., 4 Jan. 2011, *B. Goffinet* 10381 (CONN); ibid., SW of Puerto Williams, S54°58' W67°38', 150–250 m, Dec. 2018, *B. Goffinet* 14403 (CONN); ibid., Prov. of Malleco, La Araucania, W of Puren, S33°00' W73°10', 200–300 m, Oct. 1998, dense deciduous forest on steep slope with *Nothofagus*, *Aetoxicon*, *Cryptocarya*, *Lomatia* and abundant *Dendroligotrichum*, *B. Goffinet* 5430, 5455 (DUKE); ibid., near Villarrica, S39°11' W72°19', 200 m, Dec. 2008, in open *Nothofagus* forest among patchwork of fields, *J. Hollinger* 1931 (UBC); ibid., Region X, Parque Nacional Alerce Andino, along trail to Laguna Sargazo, S41°31' W72°35', 366 m, Feb. 2006, moss over wood, *T. Wheeler* & *P. Nelson* 1093, 3826 (CONC); ibid., Senda Darwin Biological Research Station, S41°53' W73°40', 100 ft, Jan. 2006, *T. Wheeler* & *P. Nelson* 89 (CONC); ibid., La Reserva Costera Valdiviana, S40°6' W73°29', Jan. 2008, *T. Wheeler* & *P. Nelson* 4362 (CONC); ibid., Prov. Magallanes, Brunswick Peninsula, SW of Punta Arenas, Reserva Forestal Labuna Parillar, S53°05' W71°, 450 m, Nov. 1998, *B. Goffinet* 5879 (DUKE); ibid., along road to Puerte del Hambre about 2.5 km N of Fort, S53°40' W71°, 5 m, Nov. 1998, *B. Goffinet* 5700 (DUKE); ibid., along road to Cerro Mirado, S53°09' W71°1', 150 m, *B. Goffinet* 6516 (CONN); ibid., Punta Arenas, W. of town, along road to Andino sky resort, S53°10' W71°1', 1028 ft, Jan. 2013, peatland on N side of road, dominated by *Empetrum* and *Polytrichum*, on side of *Sphagnum fimbriatum* lawn, above water level, *B. Goffinet* 11033 (CONN); ibid., Isla Navarino, S54°58' W68°12', Mar. 2000, sea level, *B. Goffinet* 6983 (CONN); ibid., Región de Los Lagos, Province of Osorno, Parque Nacional Puyehue, along gravel road U-485 from Park visitor entrance to CONAF administrative center and Antillanca, at the mirador, km 12 on road, trail going down to lookout, S40°46' W72°18', 738 m, Jan. 2015, through shaded forest and narrow grassy, wet vegetation, on mossy log, *B. Goffinet* 12721 & *C. LaFarge* (CONN); ibid., S40°47' W72°14', 916 m, Jan. 2015, narrow valley, with steep forested bank with large boulder, on soil in wet shaded steep stream bank, *B. Goffinet* 12741 & *C. LaFarge* (CONN); ibid., Prov. Chiloe, S end of Paruqe National de Chiloé, N of Cucao, S42°56' W74°06', 20 m, Mar. 2000, sclerophyllous woodland in pasture, *B. Goffinet* 7443 & *C. Cox* (CONN); ibid., Prov. Llanquihue, Parque Nacional Alerce

**Fig. 25** a, b. *Peltigera truculenta* var. *truculenta* from Chile (a. *B. Goffinet* 10433, CONN; b. *T. Wheeler & P. Nelson* 6156, CONC); c. holotype of *P. truculenta* var. *austroscabrosa* (*B. Goffinet* 10501, CONC); d. *P. truculenta* var. *austroscabrosa* from Chile (*B. Shaw* 18074, DUKE).

Andino, SE of Puerto Montt, S41°35' W72°33', 400–600 m, Mar. 2000, dense forest, on soil, *B. Goffinet* 7301 (CONN); ibid., Prov. Magallanes, Brunswick Peninsula, SW of Puerto Arenas, S53°05' W c. 71°, 450 m, Nov. 1998, mature *Nothofagus* forest, *B. Goffinet* 5840 (CONN). – France, Kerguelen Island, Baie de La Mouche, N part of Les Restanques, 1999, *R.S. Poulsen* 767 (H); ibid., Guillou Island, S49°29' E69°49', 14 m, Jan. 2014, on bare soil, *D. Ertz* 18875 (BR); Crozet Is, Base Alfred-Faune at Bay du Marin, S46°26' E51°51', 80 m, Dec. 1998, disturbed *Azorella*-grass vegetation, *U. Søchting* 9367 (H); ibid., Ile de la Possession, near Pointe de Bougainville, S46°26' E51°51', c. 150 m, Nov. 2015, mossy soil, *D. Ertz* 20574 (BR).

Notes — Our application of the epithet *truculenta* is based on Vitikainen (2002) who examined an isotype collection in M. He stated: "*P. truculenta* is characterised by a smooth, glossy upper cortex and diffuse or broad-veined or almost 'malaccoid' (non-veined) veining pattern. The underside is pale ochraceous but may be darker or black towards the thallus center. Tenuiorin aggregate, peltidactylin, dolichorrhizin and zeorin are found in this species by TLC. In these characters, *P. truculenta* is very similar to *P. hymenina*, an amphiatlantic-western North American species, which, however, tends to have a matt cortex". This description fits the material from the southern parts of South America. We confirmed that *P. hymenina* has not been found in South America. We chose the reference sequence for *P. truculenta* to be identical to the sequences of specimens from Prov. of Malleco (*B. Goffinet* 5430, 5455), not far from the type locality.

*Peltigera chilensis* was described from Chile by Gyelnik (1931) as an isidiate species. However, Vitikainen (2002) noted that no material corresponding to the original description is known from southern South America and he could not locate the type material in BP. He concluded that *P. chilensis* is very likely a synonym of *P. truculenta*. *Peltigera truculenta* is the only member of section *Polydactylon* in the southern parts of South America and subantarctic islands where it is mostly found on the ground. In this region, it can be recognised by its occidentalis-like lower surface: flat, broad and fused veins covering the entire surface towards the thallus center and often fasciculate rhizines. Rather similar thalli can be also found in *P. esslingeri*, another terricolous species in Central America and Colombia. However, *P. esslingeri* tends to develop thalli with a more pronounced neopolydactyla morphotype. The ITS data show some variation within *P. truculenta* with seven distinct haplotypes (differing by a single SNP and/or indels within ITS1 or ITS2) placed consistently by multiple species delimitation methods within a single species (Magain et al. 2017b). Populations found in two subantartic archipelagos (Crozet and Kerguelen) share the same haplotype with populations from Chile (Valvidian region and subantarctic region, Navarino Island).

The specimens with scabrous upper surfaces from Chile and Gough Island group together in the phylogeny and share the same ITS haplotype (Fig. 2). To accommodate this high degree of phylogenetic and morphological distinctness, we propose to recognise the scabrous collections as *P. truculenta* var. *austroscabrosa*. Additional material from Gough Island mentioned under *P. lyngei* (http://www.gbif.org/occurrence/1324747236 on 2017-03-13) most probably refers to *P. truculenta* var. *austroscabrosa. Peltigera lyngei* is a rare species known from Norway/Svalbard, Iceland and USA/Alaska (Vitikainen 1994a, Dillman et al. 2012), which was recently revealed to belong to the *hymenina* group (McMullin & Miadlikowska 2022). The report of *P. dolichorhiza* from Gough Island by Jørgensen (1977) likely refers to *P. truculenta*.

Two species resulting from the South American radiation of the *dolichorhiza* group escaped the New World eastwards: *P. dolichorhiza* (see note under this species) and *P. truculenta*, which reached the subantarctic Kerguelen archipelago in the southern part of the Indian Ocean, with the known easternmost locality at longitude E69°49'. This colonization event probably took place quite recently, as the subantarctic populations share the same haplotype with selected populations in Chile.

*Peltigera truculenta* seems to be rather common in southern South America, including ruderal habitats. Earlier records attributed to *P. polydactylon* likely belong to this species; see also '? *P. truculenta*' in the lichen checklist of Chile by Galloway & Quilhot (1998).

### ***Peltigera truculenta*** var. ***austroscabrosa*** Magain, Sérus., Goffinet & Miadl., *var. nov*. — MycoBank MB 845026; Fig. 25c, d

*Etymology*. The name highlights the scabrous upper surface, a feature otherwise not observed in *Peltigera* in southern South America.

*Typus*. Chile, Provincia Antártica Chilena, Comuna Cabo de Hornos, Bahia Ainsworth, S45°24' W69°38', sea level, Jan. 2011, coastal subantarctic vegetation among mosses in small depression along trail near forest edge; *B. Goffinet* 10501 (holo CONC; iso CONN, LG).

Reference sequence: OM778710.

*Thallus* lobes long (5–7 cm) and narrow (1–2 cm), thick but friable when dry, readily crumbling. *Upper surface* plane or almost plane, typically scabrous, grayish brown to dark brown when dry, olivaceous green when wet. *Vegetative propagules* not seen. *Lower surface* pale, almost white near lobe margins, with a poorly visible vein pattern and a few visible interstices; veins flattened, broad and fused, very dark toward the thallus center, not extending to the lobe tips leaving a veinless c. 1 cm wide marginal zone. *Rhizines* short, dark brown, forming a dense and continuous matt towards the thallus center, often covering large portions of the lower surface. *Apothecia* (present in a single specimen) saddle-shaped, 0.44–0.47 cm long, 0.46–0.58 cm wide, disc dark reddish brown to dark brown, with a crenate margin when young. *Ascospores* fusiform and elongated, sometimes bent or flexuose, (3–)5–7(–9)-septate, 55–95 × 3–5 μm (n = 15). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup: unknown (no sequence data available).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (major), dolichorrhizin (major), zeorin not detected, and accessory 2, 3, 4 and 7 (Fig. 13, S3).

Barcodes — ITS2 (CAGAAAC)**T**(TGGTTGG) (Fig. 9); this barcode distinguishes *P. truculenta* var. *austroscabrosa* from *P. truculenta* var. *truculenta*.

Ecology — On moss mats on the ground or at the base of small shrubs in heath vegetation.

Distribution — Chile/Provincia Antártica Chilena, Gough Island.

*Selected specimens examined*. Chile, Provincia Antarctia Chilena, Comuna Cabo de Hornos, Parque Nacional Alberto de Agostini, Isla Hoste, extreme W end of Seno Ponsonby, S end of Bahía Helada, S55°5' W69°4', 0–5 m, Jan. 2013, on *Empetrum* stems in heath, shaded, at the base of steep NW-facing slope with magellanic tundra, *B. Shaw* 18074 (DUKE). – Gough Is., south slope of Tafelkoppie, 500 m, Sept. 1999, *M. Gremmen* 99-348 (H).

Notes — The specimen from Gough Island was identified as *Peltigera* cf. *lyngei* by Vitikainen, but the type of that species is from Svalbard, and the species was recently shown to belong to the *hymenina* group (McMullin & Miadlikowska 2022). The three known specimens of *P. truculenta* var. *austroscabrosa* form the sister group of *P. truculenta* var. *truculenta* (Fig. 1, 2). If this pattern holds based on additional material, species or subspecies rank should be considered to accommodate *P. truculenta* var. *austroscabrosa*.

The upper surface of *P. truculenta* var. *austroscabrosa* is similar to *P. pulverulenta* and *P. scabrosa*. The lower surface of *P. truculenta* var. *austroscabrosa* resembles the lower surface of *P. pulverulenta* and *P. malacea* (section *Peltidea*).

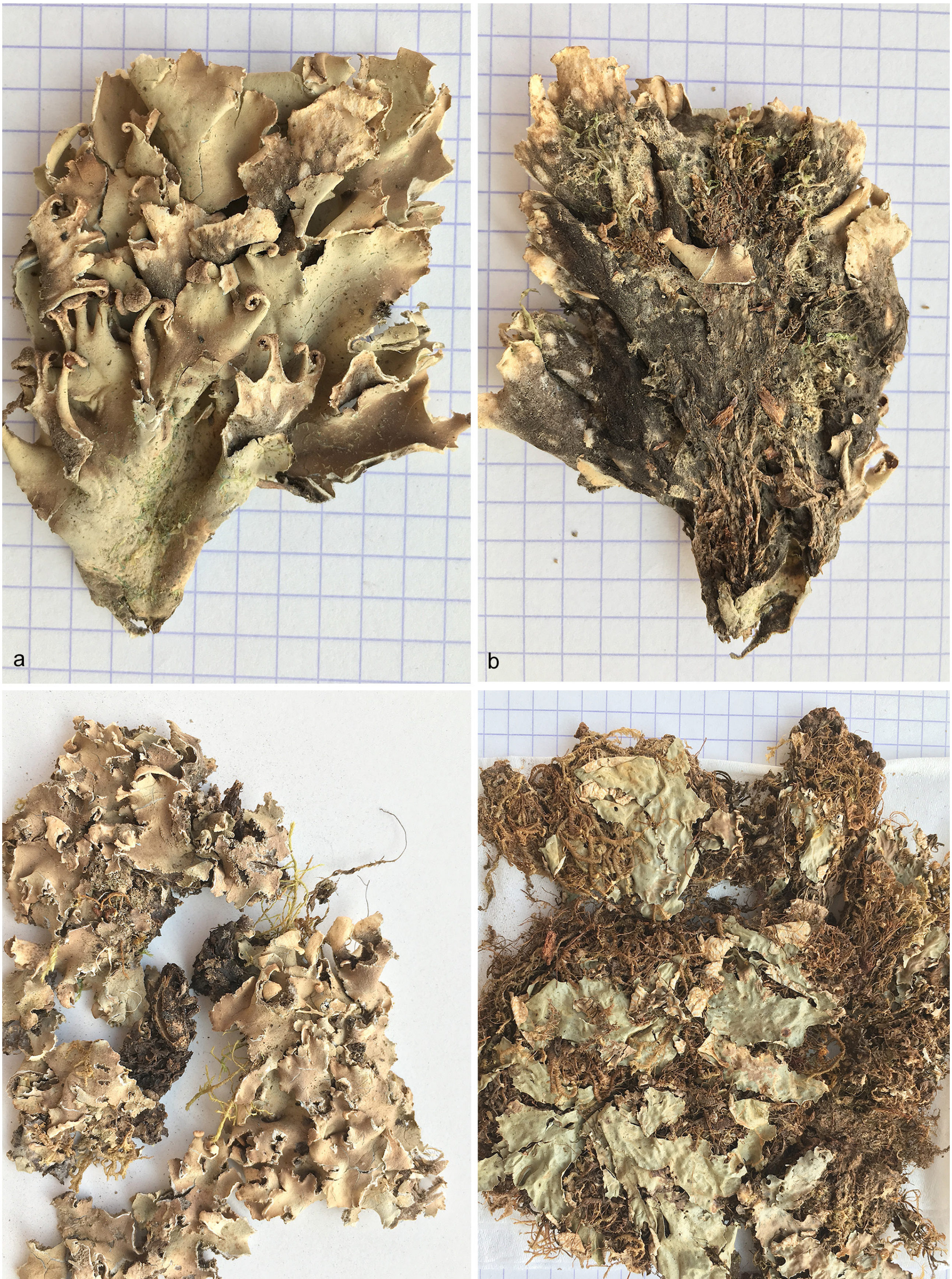

**Fig. 26** a–c. *Peltigera willdenowii*. a, b. from Colombia, holotype (*R. Lücking & B. Moncada* 34028, UDBC), a. upper and b. lower surface; c. from Venezuela (*K. & A. Kalb* 34579, DUKE). — d. *Peltigera elixii* from Papua New Guinea, holotype (*E. Sérusiaux* DNA1545, UPNG).

### ***Peltigera willdenowii*** Magain, Miadl. & Sérus., *sp. nov.* — MycoBank MB 845054; Fig. 24c, d, 26a–c

*Synonym*. *Peltigera* pulverulenta 2 in Magain et al. (2017b).

*Etymology*. This species is named in honour of German botanist Carl Ludwig Willdenow (22 August 1765 – 10 July 1812), who described the genus *Peltigera*.

*Typus.* Colombia, Cundinamarca, La Calera, Parque Chingaza, Piedras Gordas, Sector Lagunas, 3300–3600 m, *R. Lücking & B. Moncada* 34028 (holo UDBC; iso DUKE).

Reference sequence: KX897298.

Morphologically similar to *P. pulverulenta* (see description under that species), except a single population from Venezuela with granulose-isidiose lobe margins.

*Diagnosis. Peltigera willdenowii* is distinguished by its barcodes in ITS1: a seven-nucleotide motif GCCCTAC located 107 bp after the start of ITS1 between motives CTATGAA and GAAAGGGG; and a seven-nucleotide motif TGGGTTC located 129 bp after the start of ITS1 immediately preceded of motif CGAAA and followed by motif TTCTTGG

Photobiont — *Nostoc* phylogroup XIX (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (major), dolichorrhizin (major), zeorin hardly detected or absent and accessory 2 and 5 (Fig. 13, S2).

Barcodes — ITS1 (CTATGAA)**GCCCTAC**(GAAAGGGG) and ITS1 (CGAAA)**TGGGTTC**(TTCTTGG) (Fig. 9).

Ecology — On mosses on ground and on tree branches in high altitude forests.

Distribution — Colombia, Venezuela.

*Selected specimens examined*. Colombia, Cundinamarca, Choachi, Paramo de Guasca, 3000–3200 m, *R. Lücking* & *B. Moncada* 33367 (UDBC); ibid., Páramo El verjón, Parque Ecológico Matarredonda, Bogota-Choachí road, on mosses below small shrubs in a low altitude paramo, *C.J. Pardo-De la Hoz* 400 (ANDES). – Venezuela, Merida, Distr. Rangel, zwischen Santo Domingo und Apartaderos, S8°55' W70°45', 2900 m, Aug. 1989, *K.* & *A. Kalb* 34570, 34579 (DUKE).

Notes — The three species of the pulverulenta morphotype present in montane biomes of Central and South America, *P. pulverulenta*, *P. willdenowii* and *P. sipmanii* are phylogenetically closely related (Fig. 1, 2) and morphologically similar, as all typically develop a scabrous upper thallus surface (pulverulenta morphotype). No diagnostic morphological or chemical characters are available to distinguish these cryptic species. The most common and widespread is *P. pulverulenta* based on epitypification provided in this study. A single collection of *P. willdenowii* was found with granulose-isidiose lobe margins, however, this unique morphotype was not recognised by the species delimitation methods as a distinct species.

## 2. The *hymenina* group

### ***Peltigera elixii*** Magain, Goffinet, Miadl. & Sérus., *sp. nov.* — MycoBank MB 845055; Fig. 26d

*Synonyms*. *Peltigera* sp. 4 in Magain et al. (2017b).
*Peltigera dolichorhiza* s.lat. C in Sérusiaux et al. (2009).

*Etymology*. This new species is dedicated to our most distinguished colleague Prof. John A. Elix for his contribution to our understanding of lichen secondary chemistry. He examined the terpenoids produced by this species in 2008 and concluded that they are unique. J.A. Elix is a reference scientist for lichen substances (Elix 2014) and also the most prolific modern lichen taxonomist, with nearly 1200 described species (Lücking 2020; example in Elix 2016).

*Typus.* Papua New Guinea, Eastern Higlands prov., Mt Gahavisuka Provincial Park, S6°01' E145°25', 2300 m, Nov. 1995, little disturbed mossy mountain forest, dominated by *Castanopsis*, on tree, *E. Sérusiaux* DNA1545 (holo UPNG; iso LG).

Reference sequence: KX897354.

*Thallus* usually c. 5–7 cm across but sometimes smaller (1–4 cm across), lobes 0.7–1.0 mm wide, very thin and fragile. *Upper surface* smooth and usually shiny, distinctly undulating with uneven depressions; greenish beige, orange to green brown when dry, darker when wet. *Vegetative propagules* not seen. *Lower surface* pale orange near lobe margins, with a network of slightly raised, broad blackish veins and large (up to c. 4 × 2 mm), numerous, usually elliptical, whitish to pale orange interstices forming a regular network; veins extend to lobe tips but become pale orange and poorly delimited, and the marginal parts of the thallus are sometimes covered by a thin web of orange to blackish hyphae. *Rhizines* abundant, quite long (to 0.8–1 cm long), simple or penicillate, distinctly fasciculate, dark brown to black. *Apothecia* rare, finger-shaped, 3–4 mm long, disc reddish brown to dark brown, with incised-denticulate margins. *Ascospores* fusiform and elongated, usually straight, 3–7-septate, 56–72 × 4–5 µm (n = 10). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: VIIb (Magain et al. 2017 a, b).

Chemistry — (HPLC by J.A. Elix): Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); zeorin possibly present; unique set of four triterpenes always present (easily recognised on TLC plates, see Fig. 14, S2).

Barcodes — ITS1 (AAATG)**GATCCTT**(CTTGGTCT) and ITS2 (TGTCCG)**AGAGTC**(ATTGGCC) (Fig. 9).

Ecology — Mostly epiphytic but also on the ground, over mosses in montane forests in a wide altitudinal range (from 1850 to 4420 m).

Distribution — Papua New Guinea, found in seven provinces (Eastern Highlands, Madang, Morobe, Northern, Simbu, Southern Highlands and Western Highlands).

*Selected specimens examined*. Papua New Guinea, Eastern Higlands prov., Mt Gahavisuka Provincial Park, S6°01' E145°25', 2300 m, Mar. 1987, epiphyte in disturbed mossy mountain forest, *H. Sipman* 22199 (CONN); ibid., Aug. 1992, *P. Diederich* 10582 (CONN); ibid., Hogabi Village, S6°21' E145°16', 1850 m, Apr. 1982, montane forest ridge, on tree root, *H. Streimann* & *A. Bellamy* 18695 (CANB); ibid., Madang prov., Huon Peninsula, Teptep village, S5°57' E146°33', c. 2600 m, July 1992, burnt forest, on tree, *E. Sérusiaux* 13622 (CONN, LG), *H. Sipman* 35311 (B); ibid., 4 km NW of Teptep Airstrip, S5°36' E146°32', 2800–2900 m, July 1981, slightly disturbed montane rain forest on ridge, on stump, *T. Koponen* 34691 (CONN); ibid., 2 km NW of Teptep Airstrip, S5°56' E146°33', 2450–2700 m, July 1981, heavily cut montane rainsforest, on SE-sloping ridge, on trunk of *Pandanus*, *T. Koponen* 34738 (CONN); ibid., Morobe prov., Mt Kaindi Road, S7°21' E146°40', 2100 m, June 1979, montane forest, on rotting trunk, *A. Kairo* 363 (H); ibid., Northern prov., Owen Stanley Range, Myola, S9°9' E147°46', 2100–2400 m, Oct. 1995, primary mountain forest, on tree, *E. Sérusiaux* s.n. (CONN, LG) and *H. Sipman* 38261 (B); ibid., Simbu prov., Mt Wilhelm, S5°45' E145°, 4420 m, July 1967, on moss near summit, *D. McVean* 67111 (CANB); ibid., Southern Highlands prov., Onim Forestry Station, S6°9' E143°59', 2250 m, Sept. 1982, disturbed montane forest, base of young *Nothofagus*, *H. Streimann* 24549 (H); ibid., Western Highlands prov., N slopes of Sugarloaf complex, 2790 m, July 1960, montane cloud forest, epiphytic on moss, *R.D. Hoogland* & *R. Schodde* 7085 (CANB).

Notes — In the taxonomic revision of the genus from Papua New Guinea, *Peltigera elixii* corresponds to *Peltigera dolichorhiza* s.lat. C (Sérusiaux et al. 2009). *Peltigera elixii* is easily identified by a thin and brittle thallus with undulating surface and distinct depressions in addition to a set of four unique terpenoids of unusual and bright colors visible on the TLC plate after spraying with sulphuric acid and charring (Fig. 14). The upper surface of the thallus clearly represents the dolichorhiza morphotype but the marginal parts of the lower surface with a delicate network of pale orange veins and cream to orange color araneous cover resemble the polydactylon morphotype.

Another closely related species representing *P. dolichorhiza* s.lat. A in Sérusiaux et al. (2009) is known from 12 collections in Papua New Guinea. This species has also a very brittle

**Fig. 27** a–d. *Peltigera gallowayi*. a. Upper surface of specimen (*S. Stenroos* 5830, H) from New Zealand; b. specimen (*F. Högnabba* 1746, H) from New Zealand; c. holotype of *P. gallowayi* from New Zealand (*L. Tibell* 10248, H); d. upper surface of specimen (*M. Wedin* 4346, UPS) from Tasmania, Australia.

thallus and the lower surface margins similar to *P. elixii* and *P. polydactylon*. Contrary to *P. elixii*, it produces peltidactylin (sometimes absent) and zeorin. Its ITS barcode (ITS1 (AAAGCAT)**TGAATTG**(CCCAGAAG)) is slightly different from two other closely related species, *P. elixii* and *P. stanleyensis*. We could not obtain good quality sequence data to include *P. dolichorhiza* s.lat. A in the phylogenetic analyses. The photo of *P. dolichorhiza* s.lat. D (Sérusiaux et al. 2009: f. 3C) actually refers to a specimen of *P. dolichorhiza* s.lat. C (*P. elixii*).

Two collections from Philippines (Philippines, Nord Luzon, Prov. Benguet, Strasse von Baguio zum Mt. Data, 2000 m, *K. Kalb* & *A. Schrog* 12662, 12663 (DUKE)) cluster together with *P. elixii* based on their ITS sequences; however, they have a different chemistry and therefore are likely to represent an additional species in this group, which is present on many islands of the Pacific Ocean (Papua New Guinea, Philippines, Australia, New Zealand and the Hawaii Archipelago).

*Peltigera dolichorhiza* s.lat. D, a fourth species from Papua New Guinea mentioned by Sérusiaux et al. (2009) represents *P. serusiauxii* in the polydactyloid clade (Magain et al. 2020) and was referred to as *P.* sp. 11 in Magain et al. (2017a, b).

*Peltigera elixii* is currently known to associate with a single *Nostoc* phylogroup shared with other species in the dolichorhizoid clade: *P. appalachiensis*, *P. asiatica* and *P. occidentalis*.

***Peltigera gallowayi*** Magain, Miadl. & Sérus., *sp. nov.* — MycoBank MB 845056; Fig. 27a–d

= *Peltigera* sp. 3 in Magain et al. (2017b).

*Etymology.* This species is dedicated to the late David Galloway (1942–2014), a prominent lichenologist who significantly advanced our knowledge of Peltigerales in New Zealand.

*Typus.* New Zealand, Otago, Hinahina State Forest, S46°31' E169°38', 300 m, Jan. 1981, mixed forest, on trunk of fallen *Nothofagus*, *L. Tibell* 10248 (holo AK; iso H, UPS L-536372).

Reference sequence: OM955146.

*Thallus* large, usually c. 5–9 cm across, rarely up to 15 cm across, with lobes 0.5–0.9(–1.1) cm across, smaller thalli (3–4 cm across) with much narrower lobes (c. 2 mm wide) were also seen; thin and fragile or more robust; lobe margins flat or slightly raised and crisped. *Upper surface* distinctly undulated with uneven but distinct depressions if thallus very thin and papery, smooth and shiny if thallus more robust; beige to dark green, or bluish gray to dark brown when dry, dark blue when wet. *Vegetative propagules* rarely produced in form of marginal regenerating lobules, c. 0.7–1.5 mm long developed on thalli with slightly raised and crisped margins. *Lower surface* whitish to pale orange near lobe margins, becoming darker towards the center; veins quite variable, typically distinctly or slightly raised, usually pale or orange towards lobe margins, and blackish elsewhere, highly contrastive with large, numerous, usually elliptical, whitish to pale orange interstices, sometimes a dense and delicate network of pale orange veins and cream- to orange-color interstices occur towards lobe margins. *Rhizines* scattered or abundant, usually quite long (0.8–1.0 cm), dark brown to black, simple, penicillate to less frequently fasciculate. *Apothecia* usually absent, otherwise few or abundant, finger-shaped, 3–4 mm long, disc reddish brown with incised-denticulate margins. *Ascospores* fusiform and elongated, slightly bent, (5–)7-septate, 53–68 × 4–5 μm (n = 16). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: V, XX (Magain et al. 2017 a, b).

Chemistry — Tenuiorin present (major) or not, methylgyrophorate absent or minor, gyrophoric acid absent or minor; triterpenes: peltidactylin (major or minor), dolichorrhizin (major), zeorin (major or minor), and accessory 2, 3, 4 and 8 (Fig. 13, S4, S5).

Barcodes — ITS1 **CCAAAG**(CATT) (Fig. 9).

Ecology — Epiphytic on trunks and branches in pristine or disturbed forests, found also on rotting log; on soil on roadbanks in forest environments.

Distribution — Australia (New South Wales, Western Australia, Tasmania) and New Zealand (North and South Islands).

*Selected specimens examined.* Australia, Western Australia, Pemberton area, S34°27' E116°2', Aug. 2006, *S. Collins* s.n. (PERTH); ibid., New South Wales, Rocky Pic Road, Tallaganda State Forest, Great Dividing Range, S35°39' E149°39', 1200 m, Oct. 1992, *H. Streimann* 50190 (CBG, H, NY); ibid., 20 km SE of Braidwood, Monga State Forest, along Mongarlowe River, S35°38' E149°55', 730 m, Apr. 1981, *L. Tibell* 12144 (UPS L-529920); ibid., Barrington Tops National Park, 13 km W Maudville, S32°4' E152°36', 1200 m, Apr. 1981, *L. Tibell* 12324 (UPS L-529888); ibid., Tasmania, road from Zeehan to Reece Dam, S41°45' E145°5', 80 m, rain forest, Mar. 1992, on dead stem, *M. Wedin* 4346 (UPS). – New Zealand, North Island, Bay of Plenty, 16 km ESE of Opotiki, S38°3' E177°27', 85 m, Feb. 2015, open roadbank, *R. Lücking et al.* 38404 (F). ibid., Waikato, Kaimanawa Forest Park, S39°11' E175°49', 725 m, Feb. 2015, margin of well-preserved forest, *R. Lücking et al.* 38846 (F); ibid., road to Waipapa River bridge, S38°17' E175°17', 180–190 m; disturbed forest edge along road, Feb. 2015, *R. Lücking*, *B. Moncada & P. de Lange* 38220 (F); ibid., Rangipo Intake Road, S39°13' E175°47', 720–730 m; Feb. 2015, *R. Lücking*, *B. Moncada & P. de Lange* 38861 (F); ibid., Manawatu-Manganui, Pureora Forest Park, S38°39' E175°40', 550–600 m, Feb. 2015, dense podocarp forest, on tree, *R. Lücking et al.* 39039 (F); ibid., South Island, Kahurangi National Park, S41°11' E172°45', May 2010, oldgrowth forest, *F. Högnabba* 1746 (H); ibid., Fiordland National Park, S45°26' E167°41', May 2010, oldgrowth forest, on rotten trunk, *S. Stenroos* 5830 (H).

Notes — Louwhoff (2008) drew attention to the epithet *conjungens*, which was introduced for a variety of *P. polydactylon*. Vitikainen examined the type material in 1973 and assigned it (G!,digital image) to *P. dolichorhiza*. However, DNA sequences from the type specimen revealed that *Peltigera polydactylon* var. *conjungens* corresponds to *P. polydactylon* subsp. *udeghe*. As no other epithet is available, the description of a new species is needed.

*Peltigera gallowayi* is probably the morphologically most variable species examined in this study. Specimens representing typical dolichorhiza, neopolydactyla and polydactylon morphotypes are found within this lineage, which was recognised as a single species (Magain et al. 2017b). The species as circumscribed in Magain et al. (2017b) includes: 1) populations with papery thalli, a typically undulating surface with distinct depressions and long, simple rhizines on almost flat veins (dolichorhiza morphotype); 2) populations with a more robust thalli, smooth upper surface and raised veins (neopolydactyla morphotype); and 3) rare populations with small thalli characterised by smooth upper surface, raised usually lobulated lobe margins with a dense and delicate network of pale orange veins and cream- to orange-colour araneous cover on the lower surface (polydactylon morphotype).

Populations with the polydactylon morphotype are easily confused with the distantly related *P. polydactylon* subsp. *udeghe* (Magain et al. 2016), which has abundant marginal phyllidia. Specimens belonging to section *Polydactylon* in Australia have been identified as *P. dolichorhiza* or *P. polydactylon* (Louwhoff 2008, 2009) whereas in New Zealand the following four species have been recognised: *P. dolichorhiza*, *P. hymenina*, *P. neopolydactyla* and *P. polydactylon* (Galloway 2000). Specimens identified as such are likely to represent *P. gallowayi* or, in the latter case, *P. polydactylon* subsp. *udeghe*. This impressive variation was already captured by Louwhoff (2008, 2009) in her description of specimens from the two sympatric species in Australia (including Western Australia state): *P. dolichorhiza* resembling *P. polydactylon* and *P. polydactylon* with multiple morphotypes.

One of the two *Nostoc* phylogroups (phylogroup XX) associated with *P. gallowayi* seems to be restricted to Australia and New Zealand (Magain et al. 2017a).

**Fig. 28** a–c. *Peltigera hawaiiensis*. a. Holotype (*B. McCune* 22196, OSC); b. *M. Wedin* 3709, UPS; c. *R. Lücking & B. Moncada* 36353, UDBC. — d. *Peltigera hymenina* var. *hymenina* from Azores (*E. Sérusiaux* DNA1696, LG).

**Peltigera hawaiiensis** Vitik., Magain, Miadl., & Sérus., *sp. nov.* — MycoBank MB 845066; Fig. 28a–c

*Synonym*. *Peltigera hawaiiensis* ad int. in Magain et al. (2017b).

*Etymology*. The name, proposed by Dr. O. Vitikainen, calls attention to the distribution of this species, restricted to the Hawaiian Islands.

*Typus*. USA, Hawaii, NE of Kailua, N19°43' W155°55', Dec. 1994, *Metrosideros* forest, on tree, *B. McCune* 22196 (holo OSC).

Reference sequence: KX897190.

*Thallus* 5–7 cm across, with rather narrow lobes (< 0.5–0.7 cm wide), mostly thin and fragile. *Upper surface* plane or slightly undulating, usually not scrobiculate, but typically scrobiculate lobes were also observed, smooth, slightly shiny or matt, with typically upturned lobe margins, which are usually crisped and dissected; bluish gray to greenish brown when dry, dark blue gray or brown when wet. *Vegetative propagules* often present, forming rounded or dichotomously dissected squamules c. 0.1–0.3 mm long. *Lower surface* pale orange, with a poorly visible network of veins and irregular and rather large whitish interstices, which are sometimes not well delimited, when distinct veins < 0.1 mm wide, slightly raised or flat, orange to dark brown. *Rhizines* sparse, rarely abundant and scattered, pale brown to dark brown, 5–10 mm long, simple or fasciculate. *Apothecia* rare, finger-shaped, up to 3 mm long, disc reddish brown, sometimes rather pale, with a denticulate margin when young. *Ascospores* fusiform and elongated, 3–7-septate, 50–65 × 4.5–6 µm (n = 18). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup XIX (Magain et al. 2017a, b).

Chemistry — Chemotype 1: Tenuiorin absent, methylgyrophorate and gyrophoric acid major; Chemotype 2: Tenuiorin present (major), methylgyrophorate present (major), gyrophoric acid present (trace); in both chemotypes triterpenes: peltidactylin (minor to trace), dolichorrhizin (major), zeorin (trace), and accessory 2, 3 and 4 sometimes present (Fig. 14, S4, S5).

Barcodes — ITS1 (CCC)**CTATAAA**(AGGGGG) and ITS2 (TGA)**GCTTATCTGCG**(TTAGG) (Fig. 9).

Ecology — Epiphyte in natural forests (dominated by *Metrosideros polymorpha*), or on mossy ground, between 1170 and 2100 m elev. This taxon is endemic to the Hawaii archipelago and is known from montane forests where it is mostly epiphytic, but populations on mossy grounds are also found. Almost all localities where *P. hawaiiensis* has been collected are associated with *Metrosideros* forest. *Metrosideros polymorpha* (*Myrtaceae*), a tree species endemic to the Hawaiian archipelago, occupies a wide range of ecological habitats and shows remarkable phenotypic polymorphism (Izuno et al. 2016) representing an early stage of ecological speciation driven by adaptation to new and old lava flows (Stacy et al. 2014, 2017).

Distribution — Hawaii Archipelago, known from Hawaii, Kaua'i, Maui, and O'ahu islands.

*Selected specimens examined*. USA, Hawaii archipelago, O'ahu Is., Waianae Range, *Metrosideros* forest, on branch, N21°30' W58°8', 1170 m, Mar. 1990, *M. Wedin* 3709 (UPS); ibid., Hawaii Is., 12 km NE of Kailua, N9°43' W55°55', 1675 m, Dec. 1994, *B. McCune* 22196 (OSC); ibid., Maui Is., Haleakal volcano, Upper Waikamoi Preserve, introduced mixed conifer forest intermingled with *Acacia koa* and other native trees, N0°46' W56°14', 1800–2100 m, June 2013, *R. Lücking et al.* 36018, 36019 (UDBC); ibid., Kaua'i Is., western slopes of Mount Wai'ale'ale, Koke'e State Park, mostly undisturbed montane mesic forest, on *Cheirodendron*, N22°9' W159°38', 1250–1350 m, June 2013, *R. Lücking et al.* 36352, 36353 (UDBC).

Notes — The name *Peltigera hawaiiensis* has been used ad. int. by Vitikainen, and later in Magain et al. (2017a, b). Its morphology (based on multiple specimens examined) is similar to *P. hymenina* var. *dissecta* as they both have raised and crisped lobe margins, which are usually very dissected and developing marginal lobules. Several collections, however, have typical dolichorhiza or polydactylon morphotypes. This is the only representative of the whole section *Polydactylon* in the Hawaii Archipelago. Therefore, it is possible that all records of *P. polydactylon* f. *hymenina*, f. *pellucida* and f. *dolichorhiza* (Magnusson & Zahlbruckner 1943), *P. dolichorhiza*, *P. hymenina* and *P. polydactylon* (Elix & McCarthy 1998) from this archipelago represent *P. hawaiiensis*. A single specimen has been examined for its cyanobiont, which is also present in other species from the *dolichorhiza* group in South America.

**Peltigera hymenina** (Ach.) Delise, in Duby, Bot. Gall. 2: 597. 1830 — MycoBank MB 399313; Fig. 5a, 8a, 28d, 29a, b

*Typus*. Sweden, locality and collector unknown (H-Ach. 1478 ! – lectotype designated by Vitikainen 1994a: 47).

*Basionym*. *Peltidea hymenina* Ach., *Methodus*, Sectio post. (Stockholmiæ): 284. 1803.

Reference sequence: KX897198.

https://plants.jstor.org/stable/10.5555/al.ap.specimen.h9502200.

*Thallus* usually below 8–10 cm across but much larger thalli (up to 20 cm, fide Vitikainen 1994a) were also found, with lobes 0.8–1.6(–2) cm broad, fragile or robust. *Upper surface* smooth, matt or glossy, rarely slightly maculate, with lobe margins slightly but distinctly ascending and raised; grayish brown to dark brown when dry, dark bluish gray when wet. *Vegetative propagules* in form of lobules are sometimes present, sparse to abundant. *Lower surface* pale, especially the area near lobe margins which can be very pale yellow or orange, or almost white, with indistinct veins and interstices, a network of pale orange, to dark brown veins and whitish interstices is more visible towards the thallus center; in rare and scattered populations the lower surface has a strong contrast between black veins and pale interstices, which extend almost to the lobe edges. *Rhizines* scattered to abundant but not aggregated, simple to fasciculate, rather short (up to 5 mm long). *Apothecia* usually present and abundant, saddle-shaped, disc reddish brown to brown, with margins smooth or slightly incised. *Ascospores* fusiform to almost cylindrical, straight or rarely slightly bent, (3–)7-septate, 68–102 × 4–5 µm (n = 14). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: V, VIIIb, XVI, XVIII, XIX (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (major), dolichorrhizin (major), zeorin (minor), and accessory 1, 2, 4, 5 and 6 (Fig. 14, S5).

Barcodes — (TATGGG)**CTTAATAAC**(CCCTGCG) (Fig. 9).

Ecology — On mossy soil (incl. sand and clay), rocks and tree bases, in open habitats such as coastal dunes but usually in high humidity conditions, in forests and forest edges.

Distribution — Western Europe, from NW Portugal to Iceland and Central Norway, rare in the Mediterranean region and in Balkanic countries; abundant in Macaronesia (Canary Islands, Madeira and the Azores); North America: Northeastern parts (Canada/Newfoundland and Nova Scotia) and northwestern parts (USA/Oregon and Canada/British Columbia).

*Selected specimens examined*. Denmark, Jylland, Salling, Sonder Lem, Oct. 2002, *V. Alstrup* 305 (H). – France, Corsica, Vizzanova forest, N42°8' E9°8', 950 m, Sept. 2008, on mossy soil at outskirts of *Fagus* forest, *E. Sérusiaux* LG DNA 587 (LG). – Iceland, Borgr Pistilfirdi, Myrarbrekkur sunnan Kjarnalaekjar, N66°16' W15°51', 120–140 m, Aug. 2002, *H. Kristinsson* 48978 (AMNH). – Norway, Nordland, Svartisen glacier, N13°46' E66°41', 10 m, July 2010, on soil in meadow, *E. Sérusiaux* LG DNA 1492 (LG); ibid., Troms, Torsken, NNE of Ballesvika, N69°24' E17°8', 20–30 m, July 2010, over mosses debris on wall of giant boulder in boulder field in *Betula pubescens* forest with scattered *Sorbus aucuparia*, *T. Tønsberg* 40490 (BG L-89438). – Portugal, Azores, Pico, N38°30' W28°15', 245 m, Oct. 2007, large lava boulders in parkland, *E. Sérusiaux* LG DNA 298 (LG); ibid., Madeira, Casa das Queimadas, N32°47' W16°55', c. 900 m, Apr. 2007, on mossy boulders in laurisilva, *M. Dewald et al.* DNA 48 (LG). – Spain, Canary Is.,

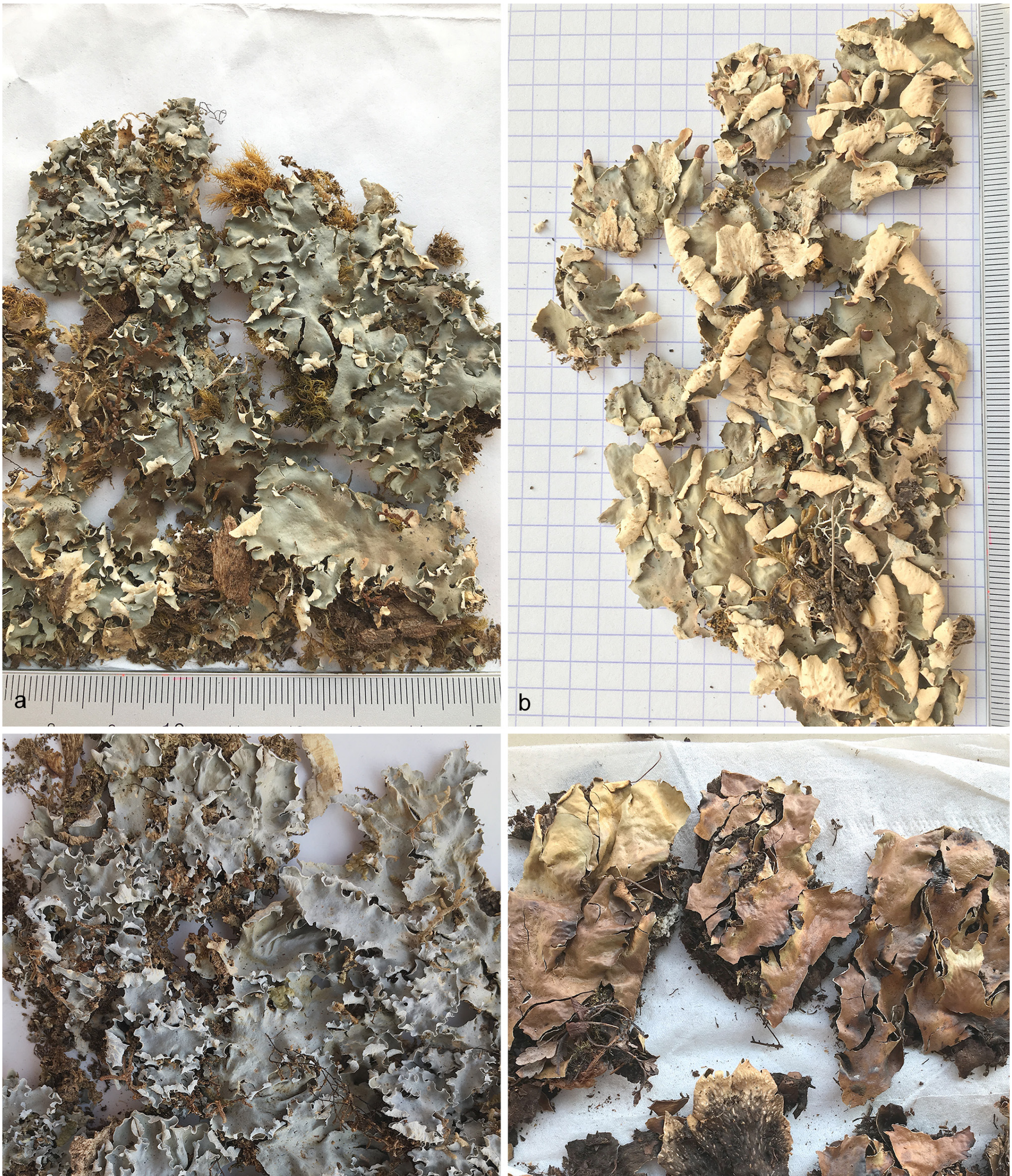

**Fig. 29** a, b. *Peltigera hymenina* var. *hymenina* from Tenerife (a. *E. Sérusiaux* DNA353, LG) and Azores (b. *E. Sérusiaux* DNA1696, LG); c. *Peltigera hymenina* var. *dissecta* from Azores (*E. Sérusiaux* DNA3950, LG). — d. *Peltigera stanleyensis* holotype from Papua New Guinea (*E. Sérusiaux* LG DNA 1534, UPNG).

Tenerife, Sierra de Anaga, N28°33' W16°11', 800 m, Apr. 2008, on mossy soil in laurisilva, *E. Sérusiaux* LG DNA 353 (LG); ibid., La Palma, Cubo de La Galga, N28°45' W17°46', 480–500 m, Apr. 2004, trunk base in laurisilva, *E. Sérusiaux* LG DNA 1696 (LG); ibid., prov. Cáceres, Acebo, Sierra de Gata, 1200 m, Apr. 1996, *G. Aragón et al.* HIMM1175 (MA-Lichen 12143). – Canada, British Columbia, Sunshine Coast, E short of Agamenon Channel on mainland, N49°42' W124°4', 10 m, July 2008, moderately shaded rock outcrop above high tide line, *C.R. Björk* 17053 (UBC); ibid., Nova Scotia, Sable Island, N43°57' W59°55', Aug. 2002, on sand with mosses, *R. Statler* S-L2 (NY); ibid., Newfoundland, Avalon Peninsula, Burry Heights Center, N47°21' W53°13', Sept. 2007, *Picea mariana-Abies balsamea* forest with sparse *Betula*, *J. Lendemer* 10397 (H). – USA, Oregon, Lane Co, west Eugene wetlands, E483850 N4879215, 130 m, Apr. 2008, on grass hummock, *D. Kofranek* 3729 (OSC); ibid., Oregon, Polk Co, Fanna meadows, N44°53' W123°38', 869 m, May 2006, open *Sphagnum* wetlands, *B. McCune* 28257 (OSC).

Notes — *Peltigera hymenina* (formerly *P. lactucifolia*) is a well-defined species, its nomenclature having been detailed by Vitikainen (1994a: 70), including the designation of a lectotype (Vitikainen 1994a: 47).

A broad spectrum of phenotypic variation among populations of *P. hymenina* was observed. In continental Europe and especially in the British Isles, large and robust thalli with a slightly undulating upper surface can be found; a distinct network of dark veins and whitish interstices on the lower surface resemble *P. vitikainenii*, which so far has not been reported from this area (Clarke 2016). In addition, populations with smaller thalli (less than 5 cm across) and small, numerous, dissected lobes grow often on soil also in the British Isles. In the Canary Islands and Madeira, populations of *P. hymenina* are abundant in the laurisilva (mossy boulders and on tree bases); they vary from typical thalli, which can co-occur with populations characterised by their very thin, bluish gray, marbled upper surface and short, simple to fasciculate rhizines (informal name '*P. friabilis* ad. int.' was used to annotate this morphotype). Species delimitation methods do not recognise these morphologically different populations as a separate species (Magain et al. 2017b). In the Azores a distinct morphotype is discussed under var. *dissecta*. A record of *P. melanorrhiza* from Spain (prov. Cáceres) by Martínez & Burgaz (1997) and Martínez et al. (1997) represent a collection of *P. hymenina* confirmed by the ITS sequence.

*Peltigera hymenina* is associated with four *Nostoc* phylogroups shared with other species within the same subclade. This species has an interesting distribution mainly in the northwestern parts of Western Europe and throughout the British Isles; it is rare in the Mediterranean region (Vitikainen 1994a) but collections from Corsica (France) at c. 950 m elev. in beech forest were validated by the ITS barcode; no reliable record is available from the Balkanic countries. It is abundant in Macaronesia (Canary Islands, Madeira and the Azores). In North America, it is confirmed from the most eastern parts of Canada (Newfoundland and Nova Scotia; see Ahti & Vitikainen 1977) and along the Pacific coast (Canada/British Columbia and USA/Oregon; Goward et al. 1995) where it is relatively rare.

### ***Peltigera hymenina*** var. ***dissecta*** (Purvis, P. James & Vitik.) Magain & Sérus., *comb. nov.* — MycoBank MB 845067; Fig. 29c, 30a, b

*Basionym. Peltigera dissecta* Purvis et al. in Arquipélago, Cienc. Biol. Marin. 11A: 7. 1993 — MycoBank MB 361857.

*Typus*. Portugal, Azores, Faial Is., Caldeira, alongside track from Canto dos Saquinhos, 580–670 m, Apr. 1992, *W. Purvis* & *P. James* (holo University of Azores, Terceira; iso BM !).

Reference sequence: KX897196.

*Thallus* forming regular rosettes 8–12 cm diam, rarely larger but usually conspicuous (on tree trunks and branches) because of their whitish to pale blue colors when wet, lobes 0.5–1.2 cm wide, fragile and easily broken; lobe margins distinctly ascending and raised. *Upper surface* smooth, matt or slightly glossy, pale grayish or brownish when dry, pale blue when wet. *Vegetative propagules* in form of marginal phyllidia or larger lobules always present, sometimes abundant, easily broken. *Lower surface* pale, pale orange to white, especially near lobe margins, with a network of pale orange to dark brown veins and whitish interstices towards the thallus center. *Rhizines* scattered to abundant but not aggregated, simple to fasciculate, usually below 5–7 mm long. *Apothecia* usually present and abundant, saddle-shaped, small (less than 2 mm long), disc reddish brown to brown, with margins smooth or slightly incised. *Ascospores* almost cylindrical (barely fusiform), straight, 7-septate, 55–95 × 4–5 µm (n = 12). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup XVI (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (minor), dolichorrhizin (major), zeorin (minor) and accessory 2, 4 and 5 (Fig. 14, S5).

Barcodes — ITS1 (ATGAACC)**TCTATGAAAG**(GGGGC) (Fig. 9).

Ecology — On tree (including small individuals) trunks, branches and shrubs in the laurisilva, mostly on native and endemic species (*Erica azorica*, *Ilex perado* subsp. *azorica*, *Juniperus brevifolia*, *Laurus azorica*, *Picconia azorica* and others), rarely inhabiting the introduced species (collected from the widely cultivated conifer *Cryptomeria japonica*).

Distribution — Endemic to the Azores, where it is known from four islands: Faial, Pico, São Miguel and Terceira.

*Selected specimens examined*. Portugal, Azores, Pico, N38°29' W28°21', 800–810 m, Oct. 2007, cloud forest, on trees, *E. Sérusiaux* DNA 274, 277 (LG); ibid., Faial, NW of the Caldeira, N38°35' W28°44', 780–800 m, July 2014, *E. Sérusiaux* DNA 3950 (LG); ibid., Terceira, Santa Barbara, Jan. 2005, *A.F. Rodrigues* (B 600173049); ibid., São Miguel, Pico da Vara, Mar. 2005, *F. Rodriguez* (B 600173186).

Notes — This taxon represents the former *P. dissecta* (Purvis & James 1993), which was found to be conspecific with *P. hymenina* but here recognised at the infraspecific level (var. *dissecta*) to acknowledge its unique morphology and ecology. In the Azores, all populations of *P. hymenina* including var. *dissecta* have a single autapomorphic substitution in the ITS1 region. Interestingly, all collections from Newfoundland and the Northwestern North America are also genetically unique (based on the ITS), but they cannot be distinguished from European populations based on morphological or chemical characters.

Another species, *P. melanorrhiza* is also endemic to this archipelago; it is placed in the scabrosoid clade as sister to two species thriving along the northern fringes of the Pacific Ocean, *P. chabanenkoae* and *P. nigriventris* (Fig. 1, 3).

### ***Peltigera stanleyensis*** Magain, Goffinet, Miadl. & Sérus., *sp. nov.* — MycoBank MB 845068; Fig. 7a, 29d

*Synonyms. Peltigera* sp. 5 in Magain et al. (2017b).
*Peltigera dolichorhiza* s.lat. B in Sérusiaux et al. (2009).

*Etymology*. This new species is named after the Owen Stanley range, an impressive mountain belt in Papua New Guinea where the type specimen of this species was found in the pristine montane forest.

*Typus*. Papua New Guinea, Northern Prov., Owen Stanley Range, Myola, S9°8' E147°47', 2700 m, Oct. 1995, in tree fern grassland in deep valley (frost hollow), *E. Sérusiaux* LG DNA1534 (holo UPNG; iso LG).

Reference sequence: KX897353.

*Thallus* conspicuous and quite large, 8–12(–15) cm across, lobes typically linear and almost unbranched (1–1.8 cm wide), brittle when dry; lobe margins almost always sharp-broken in herbarium packets and exposing medulla and photobiont

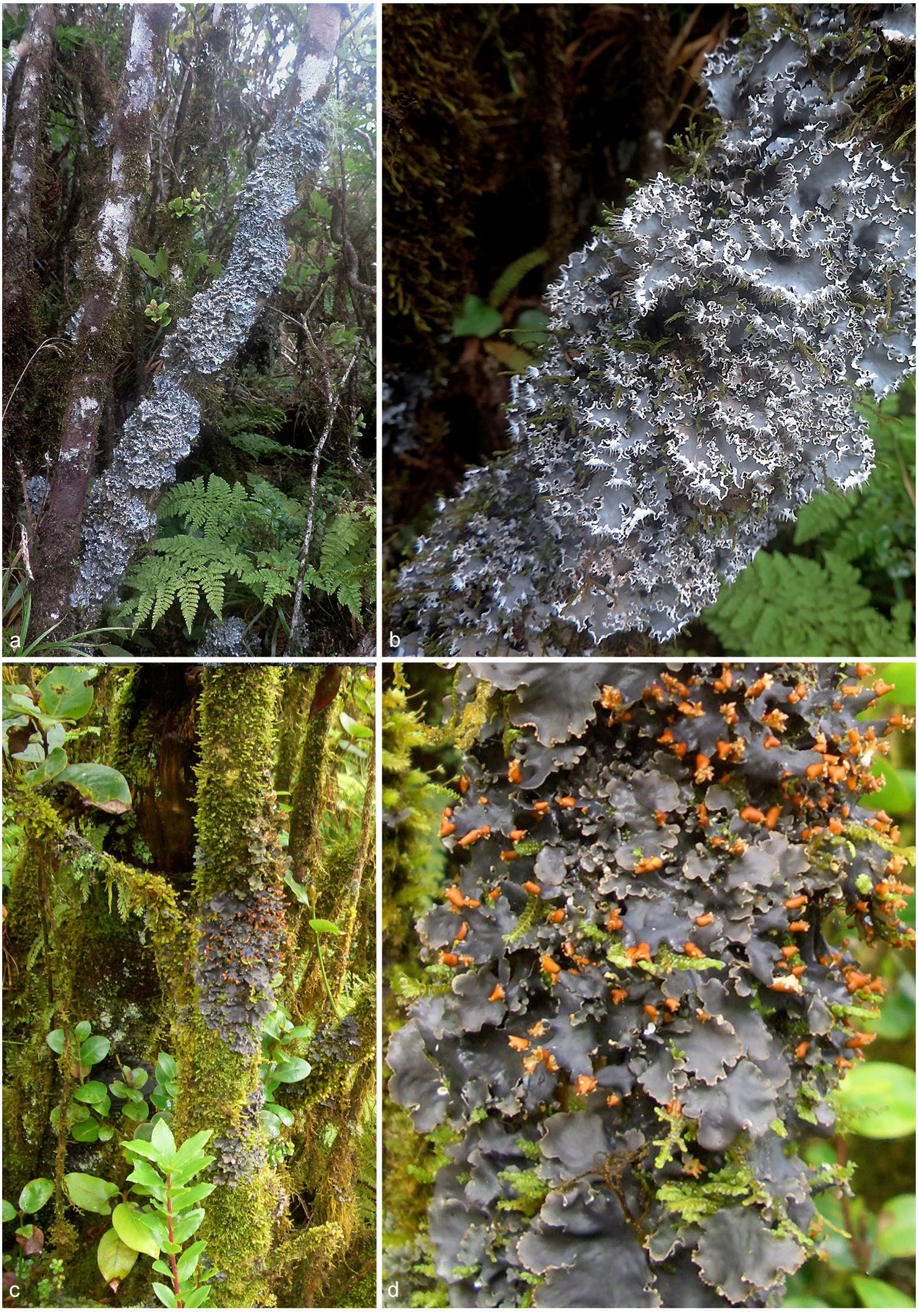

**Fig. 30** Pictures of endemic *Peltigera* taxa from the Azores. a, b. *Peltigera hymenina* var. *dissecta*; c, d. *Peltigera melanorrhiza*.

layer, otherwise flat, slightly or distinctly involute. *Upper surface* smooth and typically shiny, greenish brown to dark brown when dry, dark brown when wet. *Vegetative propagules* not seen. *Lower surface* pale orange brown near lobe margins and becoming black towards thallus center where the broadly fused veins tend to cover the whole surface and progressing outwards to a network of orange veins interrupted by small interstices, sometimes covered by a thin brownish araneous layer. *Rhizines* few or abundant, scattered, dark brown to black, 0.5–0.8 mm long, penicillate to fasciculate. *Apothecia* few or absent, almost flat to saddle-shaped, c. 3 × 2 mm, disc reddish brown, margins slightly denticulate. *Ascospores* fusiform to almost cylindrical, straight or rarely slightly bent, (3–)7-septate, 68–102 × (4–)4.5–5 µm (n = 14). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup X and unassigned haplotype (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (major) and zeorin (minor); dolichorrhizin never present, and accessory 2 possibly present (Fig. 14, S5).

Barcodes — ITS1 (TTCTTC)**TTTGTCTC**(ACACAC) and ITS1 (AAAATTC)**AATAATATTTG**(ATGTCTG) (Fig. 9).

Ecology — On tree ferns in montane forests. The type collection grew on a tree fern trunk in a tree fern forest at 2700 m, in a deep valley in the Owen Stanley Range, characterised by rare but acute frosts and irregular fires. The collection from the second locality was also obtained from the trunk of a tree fern at 3250 m, in the Huon Peninsula.

Distribution — Papua New Guinea/Northern and Morobe province.

*Specimens examined.* Papua New Guinea, Northern Prov., same locality as the type (LG, two other collections, all collections made on different fern 'tree trunks'); ibid., *H. Sipman* 38337 (B, CONN); ibid., Morobe prov., Mt Sarawaket Southern Range, 4 km SE of Lake Gwam, S6°21' E147°9', 3250 m, July 1981, subalpine forest, on trunk of tree fern, *T. Koponen* 32070 (H).

Notes — *Peltigera stanleyensis* develops the stanleyensis morphotype. Its brittle thallus with an undulating upper surface is similar to the typical dolichorhiza morphoptype but differs by its larger thallus size (up to 15 cm across) with conspicuous elongated lobes, greenish brown to dark brown color and typically shiny upper surface. The collection from Mt Sarawaket (*Koponen* 32070) is morphologically and chemically (produces peltidactylin and zeorin) very similar (Sérusiaux et al. 2009) and it is tentatively assigned to this species, although the ITS sequence for this specimen is not available. *Peltigera massonii*, an endemic species of South America, has a very similar thallus, especially of its brown and shiny upper surface. Amongst other species occurring in Papua New Guinea, *P. sumatrana* from polydactyloid clade is similar to *P. stanleyensis* but has typically saddle-shaped apothecia and a different chemistry (dolichorrhizin always present in large quantity).

From the two *Nostoc* haplotypes associated with this species, one is unique and the other one belongs to a phylogroup detected also in *P. asiatica*, *P. holtanhartwigii* and *P. mikado.*

## 3. The *pacifica* group

### ***Peltigera appalachiensis*** Magain, Miadl. & Sérus., *sp. nov.* — MycoBank MB 845069; Fig. 8d, 31a–d

*Synonym*. *Peltigera neopolydactyla* 1 in Magain et al. (2017b).

*Etymology*. This new species is named after the Appalachian Mountains in the eastern North America, which are famous for their diverse lichen flora and where this species is abundant and shows the greatest genetic diversity within its geographic range.

*Typus.* USA, North Carolina, Nantahala National Forest, Jackson Co, Chatooga River Gorge, along the Bull Pen Road, N35°2' W83°4', elev. 3150 ft, Sept. 2011, on mossy vertical rocks along the road, *J. Miadlikowska et al.*, Sept. 2011-P654 (holo DUKE).

Reference sequence: OM339151.

*Thallus* large (8–10(–12) cm across), sometimes forming ample colonies of large thalli, robust and slightly fragile when dry. *Upper surface* rarely flat, more typically slightly undulating, with wrinkles and bumps, sometimes in part crisscross-corrugate, otherwise smooth, matt; lobe margins flat or raised or involute; gray or bluish gray to gray brown when dry, either emerald green when wet (populations from boreal forests and alpine-artic regions) or vivid brown to bluish gray (populations from temperate forests in the Appalachian Mts). *Lower surface* whitish to pale orange near margins, with almost flat diffuse veins which transition to black towards the thallus center and form a network delimiting regular or irregular, various size interstices; a pale brownish araneous layer covering the surface near lobe margins present. *Rhizines* abundant, long (8–15 mm), usually simple but fasciculate on robust thalli. *Apothecia* frequent, finger-shaped, up to 3–5 mm long, disc reddish brown, with a denticulate margin. *Ascospores* fusiform and elongated, straight, 5(–7)-septate, 56–72 × 4–5 µm (n = 13). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: VIIa, VIIb, VIIc (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (major), dolichorrhizin (major to trace), zeorin (major to trace) and accessory 1, 2 and 3 (Fig. 14, S6).

Barcodes — ITS1 (GGGATAA)**GAAAGACTATGAACCT** (CTTATGA) (Fig. 9).

Ecology — On rock outcroups and boulders, on mosses or on ground in humid forests.

Distribution — The boreal zone (incl. USA/Alaska, Canada/Québec and British Columbia, Norway, Russia/Komi, Sakha Republic), the Great lakes region (USA/Wisconsin, Michigan) and the Appalachian and Ozark Mountains (USA/North Carolina, South Carolina, West Virginia, Tennessee, Arkansas, Alabama, Missouri, Pennsylvania, Vermont, Connecticut).

*Selected specimens examined*. Canada, Québec, Lake Manicouagan, N50°56' W68°58', 465 m, July 2011, boreal forest, *J. Miadlikowska* & *F. Lutzoni* W25-C2-DNAP313 (DUKE); ibid., Québec, Sept-Rivières County, Côte-Nord, N51°8' W66°3' (E100 C1), July 2011, boreal forest, Canopy cover 90 %, *J. Miadlikowska* & *F. Lutzoni* s.n. (DUKE); ibid., Alberta, Seba Beach, N53°33' W114°44', *B. Goffinet* 3063 (CONN); ibid., Rocky Mountains, Wilmore area, N53°50' W119°15', June 2009, on rock in lower alpine ridge, *C.R. Björk* 18660 (UBC); ibid., Icefields Parkway at pass near Peyto Lake, N51°43' W116°30', 2074 m, July 2011, on ground in old spruce forest by small lake, *J. Hollinger* 3910 (UBC); ibid., British Columbia, Peace River Valley, S of Hudsons Hope, N55°58' W121°55', Sept. 2008, on ground in muskeg, *C.R. Björk* 16545 with *T. Kohler* (UBC). – USA, Alaska, Fairbanks North Star Co, N65°11' W147°30', 732 m, July 2011, open *Picea* forest, on forest floor, *B. McCune* 31327 (OSC.); ibid., N64°42' W148°18', c. 900 ft, *B. Goffinet* 9424 (CONN); ibid., North Carolina, Nantahala National Forest, Jackson Co, Chatooga River Gorge, Government/Iron Bridge, N35°1' W83°8', Sept. 2011, *J. Miadlikowska et al.* 10 Sept. 09.2011-P640 (DUKE); ibid., Haywood County, Great Smoky Mountains National Park, Boogerman Trail, N35°37' W83°6', 850 m, Dec. 2009, on mossy logs in very moist old-growth cove forest along large creek, *J. Hollinger* 668 with *S. Merlo* (UBC); ibid., Arkansas, Madison Co, Boston Mountains, Dabney Creek, N35°52' W93°50', 457 m, Nov. 2010, on mossy rock on sides of gorge above waterfall, *J. Hollinger* 1766, 1781 (UBC); ibid., Alabama, Dekalb Co, Buck's Pocket State Park, 600–800 ft, *B. Goffinet* 5209 (CONN); ibid., Wisconsin, Douglas Co, Brule, *J.W. Thompson Jr.* (DUKE 0185850); ibid., South Carolina, Newberry Co, N34°26' W81°40', *W.R. Buck* 31548 (NY); ibid., West Virginia, Pocahontas Co, Watoga State Park, N38°8' W80°12', c. 610–760 m, *R.C. Harris* (NY); ibid., Missouri, Dade Co, Bona Glade Natural Area, N37°33' W93°41', *W.R. Buck* 48653 (NY); ibid., Pennsylvania, Bald Eagle State Forest, N40°58' W77°10', *J.C. Lendemer* 25238 (NY 01216935); ibid., Vermont, Essex County, Town of Averill, N44°59' W71°41', *R.C. Harris* 54602 (NY 01041851); ibid., Michigan, Huron Mts, June 2013, *J. Miadlikowska et al.* s.n. (DUKE); ibid.,

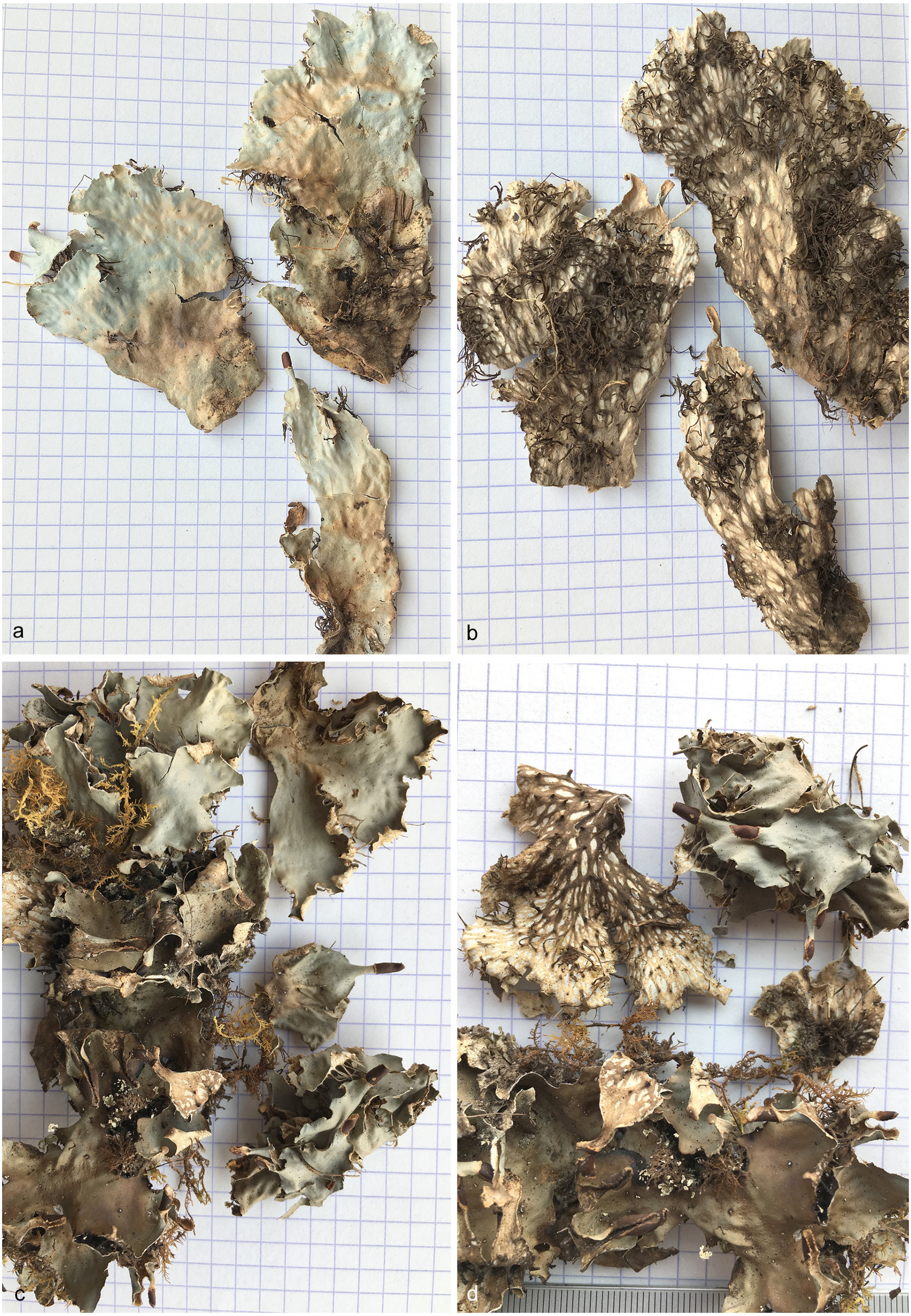

**Fig. 31** a–d. *Peltigera appalachiensis*. a, b. from Québec, Canada (*J. Miadlikowska & F. Lutzoni* W25-C2-DNAP313, DUKE), a. upper and b. lower surface; c, d. holotype from North Carolina, USA (*J. Miadlikowska et al.* 10.09.2011-P654, DUKE), c. upper and d. lower surface.

Tennessee, Sevier Co, Great Smoky Mountains National Park, Appalachian Trail west of Indian Gap, N35°37' W83°27', 1700 m, June 2011, on rotting log in mixed conifer and birch forest on north slopes of high elevation ridge, *J. Hollinger* 2943 (UBC). – Russia, Sakha Republic, Verkhoyansk District, N67°25' E134°62', 600–700 m, *T. Ahti* 65064 (H); ibid., Komi Republic, Gorod Inta, Yugyd Va National Park, old growth *Larix-Picea-Betula* forest near the Orlinoe tourist camp, N65°25' E60°41', Sept. 2019, on mosses, *I. Jüriado* 495 (TUF088262). – Norway, Ridderspranget, N61°41' E9°5', 700 m, 2011, conifer forest near river, *N. Magain* DNA-P845 (LG).

Notes — Besides the color (see below), *Peltigera appalachiensis* cannot be morphologically distinguished from *P. vitikainenii* and *P. neopolydactyla*, the two other closely related species with the neopolydactyla morphotype. However, *P. appalachiensis* is more common in boreal North America, whereas *P. vitikainenii* predominates in boreal Europe and Asia. Presence of peltidactylin and sometimes dolichorrhizin, together with zeorin as the main triterpenes detectable by the TLC, distinguishes *P. appalachiensis* from *P. neopolydactyla* (which contains only zeorin); overall, ITS is necessary for a reliable identification of these three morphologically cryptic species.

In the boreal forests in North America, five species from section *Polydactylon* have an emerald green thallus when wet: *P. appalachiensis*, recognised by its lower surface typical of the neopolydactyla morphotype (pale near the lobe margins, with a distinct network of white elliptical interstices delimited by a network of almost flat to slightly raised, or distinctly raised and convex, usually dark veins); *P. occidentalis*, recognised by its lower surface of the occidentalis morphotype (pale lobe margins with small interstices and dark veins with small whitish interstices forming a typical strong ‘black and white’ contrasting pattern towards the thallus center); and three species *P. borealis*, *P. holtanhartwigii* and *P. rangiferina* with a typically scabrous upper surface. ITS is recommended for a reliable distinction between *P. appalachiensis* and *P. occidentalis*.

*Peltigera appalachiensis* shares its *Nostoc* phylogroups with *P. occidentalis*, *P. borealis* and *P. rangiferina*. Phylogroup VIIa is responsible for the emerald green color of wet thalli in boreal forests, whereas phylogroup VIIb and VIIc give a brownish gray color to wet thalli in forests in the Appalachian and Ozark Mts. A similar switch between the *Nostoc* phylogroups resulting in a change of the color of the wet thalli in different habitats and disjunct geographical areas was also observed in *P. occidentalis*.

**Peltigera asiatica** Magain, Goffinet, Miadl. & Sérus., *sp. nov*. — MycoBank MB 845070; Fig. 4d, 32c, 33a–d

*Synonym*. *Peltigera neopolydactyla* 3 in Magain et al. (2017a, b).

*Etymology*. The name calls attention to this species’ widespread occurrence in east Asia, where it appears to be endemic.

*Typus*. Vietnam, Kontum prov., Anamese Range, Kontum plateau, Ngoclinh Mt, N15°4' E107°59' (coordinates by the authors for the Ngocling Mt summit), 1999 m, on soil, *Vo Thi Phi Giao* G06-NL86B (holo PHH; iso B).

Reference sequence: KX897247.

This species has two distinct morphotypes: dolichorhiza and polydactylon.

*Dolichorhiza morphotype*

*Thallus* large (up to 15–30 cm diam), sometimes forming patches of multiple thalli spread over large areas, lobes

**Fig. 32** Pictures of *Peltigera* in the field. a. *Peltigera chabanenkoae* in Hokkaido, Japan; b. *Peltigera hokkaidoensis* in Honshu, Japan; c. *Peltigera asiatica* in Taiwan; d. *Peltigera mikado* in Taiwan.

**Fig. 33** a–d. *Peltigera asiatica*. a, b. Holotype of *P. asiatica* from Vietnam (*Vo Thi Phi Giao* G06-NL86B, PHH), a. upper and b. lower surface; c, d. from Taiwan (*E. Sérusiaux* T69 w. *B. Goffinet*, LG), c. upper and d. lower surface.

1–1.5 cm broad, typically fragile and brittle when dry, lobe margins flat. *Upper surface* scrobiculate or undulating, with distinct, rounded or irregular shallow cavities, somewhat glossy, pale bluish gray when dry, bluish gray to brownish and distinctly concave when wet. *Vegetative propagules* not seen. *Lower surface* pale yellowish at lobe margins, with slightly raised, pale orange to yellowish veins, which become dark brown to blackish and diffuse towards the thallus center, but a regular pattern of whitish, elliptical to irregular interstices is clearly visible. *Rhizines* sparse, simple to slightly fasciculate, 0.4–1 mm long, dark brown to black including the lobe margins and thus forming a strong contrast with the pale thallus surface and pale orange veins. *Apothecia* rare to abundant, saddle-shaped, 4–8 mm long, disc light brown to reddish black, crenulate when young. *Ascospores* very long and elongated, neither flexuose, nor bent, 7-septate, 84–114 × 3.5–4 µm (n = 21). *Pycnidia* not seen.

*Polydactylon morphotype*

*Thallus* smaller (5–8 cm diam) and isolated and not covering large areas, with lobes c. 0.5 cm broad, fragile but not brittle when dry, margins flat. *Upper surface* scrobiculate or slightly undulating, without distinct shallow cavities, lobes somewhat glossy, patches of scattered, minute whitish crystals occasionally present; dark bluish gray to dark brown when dry, dark gray to brownish when wet. *Vegetative propagules* not seen. *Lower surface* pale brownish at lobe margins, with slightly raised, orange to brownish veins extending to lobe tips with distinct small pale interstices, veins becoming diffuse dark brown to blackish towards the thallus center contrasting with whitish, elliptical to irregular interstices. *Rhizines* sparse, slightly fasciculate to bush-shape, less than 5 mm long, dark brown to black. *Apothecia* not seen. *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: VIIb and X (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (major to trace), dolichorrhizin (major), zeorin (trace) and accessory 1, 2 and perhaps 3 (Fig. 14, S6).

Barcodes — ITS1 (GAACC)**CCCTTCT(**GA) and (GA)**GTGG** (GGGGGAAT), ITS2 (CAG)**GTTGTACAA**(GGTTG) (Fig. 9).

Ecology — Usually in forested mountainous areas on mossy ground, in deep shade or in more open places.

Distribution — China/Yunnan, Malaysia/Borneo, Taiwan, Vietnam.

*Selected specimens examined*. China, Yunnan prov., Lunan Co, near Shilin and Stone forest, N24°44' E103°20', 1900 m, Oct. 2002, open *Pinus yunnanensis* forest with limestone outcrops, *J. Miadlikowska* s.n. (DUKE). – Taiwan, Miaoli Co, Dayueshan National Forest Recreation Area, Siaosyueshan at the end of the road, N24°17' E121°2', 2175 m, Oct. 2016, secondary forest, on mossy soil in dense bamboo undergrowth, *E. Sérusiaux* T69 w. *B. Goffinet* (LG); ibid., Chiayi Co, Alishan National Forest area, Tashan trail, near summit, N23°32' E120°49', ± 2625 m, Oct. 2016, *Salix* forest with dense bamboo undergrowth, *E. Sérusiaux* T299, T321 w. *B. Goffinet* (LG). – Malaysia, Borneo, Sabah, Kinabalu Park; N6°3' E116°34', 3244 m, 2018, Indo-Malay tropical and subtropical moist broadleaf forest, low forest, on mosses on rocks, *N. Magain* Golife-196 (BORH).

Notes — *Peltigera asiatica* is a puzzling species as it can develop dolichorhiza or polydactylon morphotypes. Additionally, the thalli of polydactylon morphotype can have inconspicuous but noticeable patches of whitish crystals on the upper surface, which is a common character in the *nana* group in the polydactyloid clade. In Asia, both species can also be confused with *P.* sp. 8 (Magain et al. 2017a), a species complex comprising several unresolved sympatric species (China/Yunnan, Taiwan, Japan and Russia/Khabarovsk). Therefore, *P. asiatica* can only be recognised with the ITS barcode (Fig. 10). Its *Nostoc* symbionts are shared with other species from the dolichorhizoid clade. Based on the current distribution of *P. asiatica*, we expect it to occur elsewhere in the Indo-Malay region (Olson et al. 2001).

### ***Peltigera borinquensis*** Magain, Merc.-Díaz, Miadl. & Sérus., *sp. nov.* — MycoBank MB 845071; Fig. 34a–c

*Synonym*. *Peltigera neopolydactyla* 1b in Magain et al. (2017b).

*Etymology*. The epithet refers to ‘Borinquen’, the Taíno name for the island of Puerto Rico.

*Typus*. USA, Puerto Rico, Reserva Forestal Toro Negro, along trail beside stream of watershed of Salto Inabon, from Hwy 143 at KM 18.6 at Monte Jayuya, N18°10' W66°38', 1210–1265 m, Jan. 1992, humid palm brake, *R.C. Harris* 27299 (NY).

Reference sequence: MT488027.

*Thallus* 4–5 cm across, with lobes 0.5–1 cm across, thin and fragile, with flat lobe margins. *Upper surface* slightly undulating to scrobiculate, smooth, slightly shiny or matt; bluish grey or brownish, dark blue grey or brown when wet. *Vegetative propagules* not seen. *Lower surface* pale, with a poorly visible network of slightly raised or flat, orange to dark brown veins and whitish, irregular interstices. *Rhizines* sparse, scattered, pale brown to dark brown, 5–10 mm long, simple or fasciculate. *Apothecia* rare, few when present, saddle-shaped, with a slightly denticulate margin; disc c. 3–4 mm long, pale orange brown. *Ascospores* fusiform and elongated, straight, 5–7-septate, 80–85 × 3–4 µm (n = 17). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup VIIb (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (minor) and gyrophoric acid (trace); triterpenes: peltidactylin (minor), dolichorrhizin (major), zeorin (trace) and accessory 2 and 4 (Fig. 15, S6).

Barcodes — ITS1 (TTT)**TTGTTGT**(CTGAACA) ITS2 (GAAA)**CCTAGT**(TGGATGT) (Fig. 9).

Ecology — On boulder on mosses or on soil.

Distribution — Panama, Peru and USA/Puerto Rico.

*Specimens examined*. Panama, Chiriqui Province, PN Volcan Baru, Sendero Copete, N8°49' W82°31', 2592 m, July 2016, *N. Magain* NM113 (DUKE). – USA, Puerto Rico, El Yunque National Forest, Rio Grande near El Toro peak summit, N18°16', W65°50', 1052 m, July 2018, on tree in lower montane rain forest, *J.A. Mercado-Díaz* 3655 (F); ibid., same locality as holotype, *R.C. Harris* 27328 (NY). – Peru, Pasco Region, Prov. Oxapampa, Parque Nacional Yanachaga-Chemillen, Selva alta, North exposure, S10°33' W75°22', 2356 m, July 2010, on boulder with mosses, *E. Gaya* 07.14.10-19 (DUKE).

Notes — *Peltigera borinquensis* develops the typical dolichorhiza morphotype and it is sympatric in Central and South America with other morphologically similar species (*P. dolichorhiza*, *P. esslingeri*). Except for its preference for terricolous habitats, it is morphologically and chemically indistinguishable from *P. dolichorhiza*, and therefore the ITS barcode is necessary for its identification. For distinguishing *P. borinquensis* from *P. esslingeri*, see Notes under the latter species.

### ***Peltigera mikado*** Magain, Goffinet, Miadl. & Sérus., *sp. nov.* — MycoBank MB 845072; Fig. 4c, 32d, 35a–d

*Synonym*. *Peltigera neopolydactyla* 2b in Magain et al. (2017b).

*Etymology*. This new species is named after the mikado game (so the epithet is a noun in apposition), which was first recorded in Buddhist writings of the 5th century BC and now it is known worldwide.

*Typus*. Taiwan, Hualien Co, Taroko National Park, along trail to Little Qilai Mt, N24°08' E121°17', ± 3090 m, Oct. 2016, open bamboo grassland near exposed rocks outcrops with *Rhododendron* shrubs and *Juniperus squamata*, *E. Sérusiaux* T266 & *B. Goffinet* (holo TAIE; iso LG).

Reference sequence: MT488051.

This species has two distinct morphotypes: dolichorhiza and polydactylon. Dolichorhiza morphotype can be distinguished by the size and fragility of the thallus and its dolichorhizoid lower side with long and simple rhizines vs the polydactyloid lower side with short, fasciculate, bush-like rhizines.

**Fig. 34** a–c. *Peltigera borinquensis.* a, b. from Peru (*E. Gaya* 07.14.10-19, DUKE), a. upper and b. lower surface; c. holotype from Puerto Rico (*R. Harris* 27299, NY). — d, e. *Peltigera pacifica* from British Columbia, Canada (d. *O. Vitikainen* 13080; e. *B. Goffinet* 3135, CONN).

**Fig. 35** a–d. *Peltigera mikado*. a. Holotype from Taiwan (*E. Sérusiaux* T266, TAIE); b. from Yunnan, China (*B. Goffinet* 10115, CONN); c, d. from Honshu, Japan (*E. Sérusiaux* s.n., LG), c. upper and d. lower surface.

*Dolichorhiza morphotype*

*Thallus* large (up to 15 cm diam) with lobes c. 1 cm broad, typically fragile and brittle when dry; lobe margins flat. *Upper surface* undulate or scrobiculate with distinct, rounded or irregular shallow cavities, somewhat glossy, without pruina or whitish crystals, pale bluish gray, becoming dark bluish (slate color) to brownish when wet. *Vegetative propagules* not seen. *Lower surface* pale yellowish at lobe margins, with slightly to strongly raised, orange veins becoming dark brown to blackish towards the thallus center, diffuse or clearly delimited, forming a regular pattern of whitish, sometimes large (3 × 2 mm), elliptical to irregular interstices. *Rhizines* abundant, simple to slightly fasciculate, 0.4–1 mm long, dark brown to black including marginal parts and thus forming a strong contrast with the pale undersurface. *Apothecia* rare to abundant, saddle-shaped, 4–6 mm long, disc light brown to reddish black, crenulate when young. *Ascospores* very long and elongated, neither flexuose, nor bent, 5–7-septate, 71–105 × 3.5–5 µm (n = 19). *Pycnidia* not seen.

*Polydactylon morphotype*

*Thallus* smaller (5–8 cm diam) with lobes c. 0.5 cm broad, fragile and rather brittle when dry; margins sometimes clearly raised and slightly undulating. *Upper surface* scrobiculate or slightly undulating, somewhat glossy, patches of scattered, minute whitish crystals present; dark bluish brown or grayish when dry, pale greenish brown (olive color) to dark gray or brownish when wet. *Vegetative propagules* not seen. *Lower surface* pale brownish to orange at lobe margins, with slightly or strongly raised, orange to brownish veins, extending to the lobe tips where small pale interstices are clearly visible, resembling typical polydactylon lower surface near the lobe edges (incl. a brownish red araneous hyphal layer), veins becoming dark brown towards the center forming a distinct contrast with poorly delimited but whitish, elliptical to irregular interstices. *Rhizines* sometimes absent, but usually abundant, simple to typically fasciculate, sometimes fluffy, 3–5 mm long, dark brown to black. *Apothecia* not seen. *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: X and VIIb (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (major to minor) and gyrophoric acid (trace); triterpenes: peltidactylin (major to minor), dolichorrhizin (major), zeorin (major to minor) and accessory 1, 2, 5 and 8 (Fig. 15, S6, S7).

Barcodes — ITS1 (ACC)**TCTCTTA**(TGAAG) (Fig. 9).

Ecology — On mossy ground or mossy rocks, often in deep shade, including rocks near waterfall; always in forested localities, including degraded forests.

Distribution — China/Yunnan and Jilin, Taiwan, Japan/Honshu and Hokkaido Is, Kochi, Russia/Khabarovsk.

*Selected specimens examined*. China, Yunnan prov., Lijiang Prefecture, Jianchuan Co, Shi Baoshan Mt, N26°22' E99°50', ± 2440 m, July 2010, forest with *Pinus yunnanensis*, *Quercus* and *Rhododendron*, *B. Goffinet et al.* 10115 (CONN); ibid., Jilin prov., Erdaobaije county, c. 30 km from Erdaobcun, N42°12' E128°10', c. 1100 m, *M. Sohrabi* 16650 (MS Herb.). – Japan, Honshu, Kii Sanchi peninsula, SE of Koyasan, N34°11' E135°36', 750 m, Apr. 2013, disturbed forest by a small river, on mossy ground, *E. Sérusiaux* LG 3305, 3309 (LG, TNS); ibid., Kochi, Ino-cho Town, Teragawa, N33:45.09-16 E133:11.48-54, 750–770 m, Oct. 2006, *G. Thor* 21279 (UPS 383558); ibid., Hokkaido, Kawakami district, Shibecha experimental forest, N43°21' E144°40', c. 100 m, Aug. 2019, old forest with lots of dead wood, *N. Magain et al.* 8076a (LG); ibid., Urakawa-gun, Urakawa, Nobuka, near Petekari Sanso, N42°29' E142°49', 636 m, Aug. 2019, *N. Magain et al.* 8087 (LG). –Taiwan, Miaoli Co, Dayueshan National Forest Recreation Area, Siaosyueshan at the end of the road, N24°17' E121°2', 2175 m, Oct. 2016, secondary mixed wood forest, on wet ditch, *E. Sérusiaux* T74 with *B. Goffinet* (LG); ibid., Nantou Co, Sun-Link-Sea Forest and Nature Resort, N23°37' E120°48', ± 1650 m, Oct. 2016, on mossy rocks near Songlong Rock Waterfall, *E. Sérusiaux* T103 with *B. Goffinet* (LG); ibid., Hualien Co, Taroko National Park. Off Hwy 14a, along trail to Little Qilai Mountain, N24°08' E121°17', ± 3090 m, Oct. 2016, natural vegetation with open bamboo grassland, *Abies kawakamii* forest with dense bamboo undergrowth, *Rhododendron* forest and exposed rock outcrops with *Juniperus squamata*, *E. Sérusiaux* T266, 267, 440 with *B. Goffinet* (LG), *B. Goffinet* 13580 w *E. Sérusiaux* (CONN). – Russia, Khabarovsk Territory, Bol'shekhetzkhirskii State Reserve, Sosnenskii sector, c. 48 km southwest of Khabarovsk, around Sosnenskii Cabin at Sosnenskii Creek, along Sphinx Trail, N48°14' E134°47', 534 m, Sept. 2013, *F. Lutzoni* & *J. Miadlikowska* 06.29.2013-P3032 (DUKE).

Notes — *Peltigera mikado* occurs in the Indo-Malay and Palearctic regions. Similar to closely related *P. asiatica*, *P. mikado* develops two distinct morphs. The polydactylon morphotype often bears pale to white incrusted patches on the upper surface, a common feature in the *nana* group in the polydactyloid clade. In Asia both species can also be confused with *P.* sp. 8 (Magain et al. 2017a), a species complex in need of further study. Therefore, *P. mikado* can only be recognised with the ITS barcode (Fig. 10).

### ***Peltigera pacifica*** Vitik., Ann. Bot. Fenn. 22: 294. 1985 — MycoBank MB 102980; Fig. 34d, e

*Typus*. Canada, British Columbia, 10 km N of Kitsumkalum Lake, N54°55' W128°51', 150 m, shady secondary growth of *Pinus contorta-Tsuga* forest, Aug. 1981, terricolous, road bank of forest edge, *T. Goward* 81-2025 (holo UBC n.v.; iso BM !, CANL, H !, US).

Reference sequence: KX897284.
https://plants.jstor.org/stable/10.5555/al.ap.specimen.ubcl16994.

*Thallus* usually small (c. 1–3 cm diam) forming rounded multithalli patches (c. 3–10 cm across), sometimes up to c. 30 cm diam, lobes 0.5–1 cm broad, usually rather thick and robust, although smaller thalli can be quite thin and rather fragile; lobe margins typically raised. *Upper surface* scrobiculate or undulating, smooth, somewhat glossy and shiny; bluish gray when dry and dark blue, from lead-colored to violet when wet. *Vegetative propagules* generally abundant in form of phyllidia or small lobules, 0.3–0.7 mm diam, friable, readily breaking. *Lower surface* very pale, whitish to ochraceous; veins pale, brown to dark brown towards the thallus center and light ochraceous towards lobe margins, 0.5–1 mm wide, raised and somewhat angular in cross section, forming a distinct network with rounded to ellipsoid, sometimes rhombic interstices, which are clearly visible towards the thallus center. *Rhizines* not abundant but regularly distributed, becoming sparse towards the thallus center, 3–9 mm long, dark brown, simple to fasciculate, sometimes branched. *Apothecia* usually present, saddle-shaped, 5–6 mm long, disc light brown to black. Excipulum outer surface smooth. *Ascospores* fusiform and elongated, slightly flexuose or not, 5–7-septate, 68–80 × 3.5–4 µm (n = 10). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup XIII (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (minor) and gyrophoric acid (trace); triterpenes: peltidactylin (minor), dolichorrhizin (major), zeorin (trace) (Fig. 15, S7).

Barcodes — ITS1 (ACTAT)**GAACCCCTATGAAG** (GGGGGG) and ITS2 (TGGC)**CAAAATTTTTTA**(CTTT) (Fig. 9).

Ecology — Terricolous or muscicolous, on rocks, fallen logs, or tree trunks (mostly the lower parts), usually in wet and shady habitats; reported from sea level to c. 1400 m elev.

Distribution — Northwestern North America, from Alaska to Oregon, Washington and Idaho, including British Columbia in Canada. The Consortium of North American Lichen Herbaria (http://lichenportal.org/portal/taxa/index.php?taxon=55987) features one collection from California, Monterey, Santa Lucia Mountains, which represents its southernmost known occurrence.

*Selected specimens examined*. USA, Oregon, Linn Co, Willamette National Forest, old forested lava flow near McKenzie River, N44°21' W122°, 810–920 m, Aug. 2000, *B. Goffinet* 7937 (CONN); ibid., Coos Co, c. 13 km SW of Coos Bay, Cape Arago State Park, N43°18' W124°24', 0–30 m, Aug. 2000, *B. Goffinet* 8016a (CONN); ibid., Benton Co, 1 km south of Alsea Summit, N44°28' W123°30', 448 m, May 2005, *B. McCune* 27796 (OSC); ibid., Washington, Skamania Co, Curly Creek, 4 mile east of Pine Creek information center, N46°3' W121°58', July 1993, *R.I. Hastings* C.93.4.225 (PMAE); ibid., Idaho, Clearwater Co, Dworshak Reservoir, Cold Springs Trail, about 0.5 mile east of Ove Creek, N46°36' W116°12', 160 ft, June 2000, basalt landslide in *Abies grandis* forest, *K.L. Gray* 1863 (NY01106901). – Canada, British Columbia, Vancouver Island, 5 km SW of Bamfield, N48°47' W125°10-11', sea level, Aug. 1994, on lying mossy log at edge of oldgrowth coniferous rain forest, *O. Vitikainen* 13080 (H); ibid., Mohun Creek, N50°6' W125°26', 140 m, Aug. 2008, on east-facing cliffs, *C.R. Björk* 17500 with *T. Kohler* (UBC); ibid., NE of Cedar, N49°10' W123°, 5 m, Sept. 1992, on tree, *B. Goffinet* 3135 (DUKE); ibid., East coast, S of Nanaimo, NE of Cedar, N49°10' W123°, 5 m, Nov. 1992, trail through tall coastal forest with *Tsuga heterophylla* and deciduous trees, *B. Goffinet* 3119, 3135 & 3137 (CONN); ibid., Coast Ranges, Upper Tahumming River, N50°26' W124°40', Sept. 2009, mossy bank at streamside, *C.R. Björk* 19562 with *T. Kohler* (UBC); ibid., Monashee Mountains, Northeast slope of Malton Range, West side of Kinbasket lake, N52°35' W118°58', June 1991, acidic bedrock cliffs surrounding tarn lake in *Abies lasiocarpa-Picea engelmanii* and low alpine tundra with *Empetrum* and *Cassiope*, *B. Goffinet* 1443 (CONN).

Notes — *Peltigera pacifica* was described by Vitikainen (1985). It displays the neopolydactyla morphotype and in North America, it is the only species with this morphotype to produce fragile phyllidia on raised lobe margins. Other species from section *Polydactylon* in Western North America with lobules are: *P. polydactylon* subsp. *udeghe*, easily recognised by its polydactylon morphotype (Fig. 7a, b), and rare forms of *P. hymenina*, easily distinguished by their lower surface typical of the hymenina morphotype (Fig. 8a). Specimens of *P. pacifica* with sparse or poorly developed marginal phyllidia can be mistaken for *P. neopolydactyla*, *P. clathrata*, *P. nigriventris*, or sometimes *P. vitikainenii*, a rare form with raised margins (see descriptions under each species). The ITS barcodes are necessary to distinguish these species unambiguously.

*Peltigera pacifica* shares its *Nostoc* symbiont with the closely related *P. vitikainenii*, which is more widely distributed in the northern hemisphere, and with the widespread *P. membranacea* and *P. degenii* from section *Peltigera* (Magain et al. 2018).

### ***Peltigera vitikainenii*** Magain, Miadl., Goward & Sérus., *sp. nov.* — MycoBank MB 845073; Fig. 8b, 36a–d

*Synonym*. *Peltigera neopolydactyla* 2a and 2c in Magain et al. (2017b).

*Etymology*. The species is named in honour of Orvo Vitikainen, Helsinki, Finland, whose taxonomic work on *Peltigera* over many decades laid the foundation for this taxonomic treatment.

*Typus*. Norway, Akershus, Siggerud, Vangenveien, N59°48' E10°59', 250 m, July 2011, conifer forest near river, *N. Magain & E. Timdal* P384 (holo O; iso H, LG).

Reference sequence: KX897237.

*Thallus* large, 8–15 cm across, sometimes larger, robust or fragile and brittle when dry. *Upper surface* slightly undulating, with wrinkles, or scrobiculate, smooth, matt; gray or bluish gray to gray brown when dry, vivid brown to bluish gray when wet, lobe margins flat or raised, sometimes involute. *Vegetative propagules* not seen. *Lower surface* whitish to pale orange near the margins, becoming darker towards the center, with raised pale orange or brown veins forming an irregular network delimiting mostly irregular in shape and size interstices, veins becoming fused and dark toward the thallus center, a pale brownish araneous layer rarely present near the lobe margins. *Rhizines* abundant, long (8–15 mm long), usually simple or fasciculate. *Apothecia* frequent, finger-shaped, up to 3–5 mm long, disc reddish brown, with a denticulate margin. *Ascospores* fusiform and elongated, bent, 7-septate, 59–70 × 3–4 µm (n = 38). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: V, XIII, XVII (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major to absent) and gyrophoric acid (minor to absent); triterpenes: peltidactylin (major to trace), dolichorrhizin (major to absent), zeorin (trace to absent) and accessory 1, 3, 9, 10 and sometimes 5 (Fig. 15, S7).

Barcodes — ITS1 (CTTGG)**GCATATAAA**(GCTGT) and ITS1 (TATGAA)**CCTCTTATGAAGGG** (Fig. 9).

Ecology — Usually on mosses on logs or rocks in humid forests.

Distribution — Europe / Norway, Estonia, Ukraine, France, Switzerland; Canada / British Columbia; USA / Montana, Alaska; Japan / Hokkaido; Russia / Sakhalin and Khabarovsk; not known from Eastern North America.

*Selected specimens examined*. France, Cantal, W of Puy Mary, N45°8' E2°39', 1125 m, on mossy ground in *Abies-Fagus* forest, Aug. 2020, *E. Sérusiaux* s.n. (LG); ibid., Pyrénées Atlantiques, S of Tardets-Sorholus, Kakouetta gorges, July 1990, on *Corylus*, *P. Diederich* 9426 (LG); ibid., Vosges, La Bresse, near lac des Corbeaux, N48° E6°54', Sept. 2019, on mossy boulder facing the lake, *N. Magain* s.n. (LG). – Norway, Telemark, South of Amotsdal, along the Amotsdalvegen, N59°37' E8°25', 2011, *N. Magain* s.n. (LG); ibid., Buskerud, Veggli, Vegglifjellveien, N60°2' E9°7', 2011, *N. Magain* s.n. (LG). – Estonia, Põlva county, Põlva commune, Taevaskoja, N58°7' E27°4', Mar. 2017, dry boreal forest, mixed forest with pine, spruce and deciduous tree, on decaying mossy log, *I. Jüriado* (TUF088251); ibid., Ida-Viru County, Muraka Nature Reserve, on decaying log (*Populus tremula)*, N59°11' E27°10', July 2006, *P. Lõhmus* (TUF047418); ibid., Polva Co, Polva commune, Taevaskoja, dry boreal forest, mixed forest with pine, spruce and deciduous tree, N58°7' E27°4', Mar. 2017, on decaying mossy log, *I. Jüriado* (TUF 88251). – Ukraine, Transcarpathian region, Rakivka, road from Hoverla to the mountain, beech spruce forest, June 1948, on a rotten log, *Mikarya* (LE). – Switzerland, Canton de Vaud, La Dole, pessière, 1360 m, sol moussu, *M. Vust* s.n. (G 00295951); ibid., Canton de Berne, Arnensee, 1564 m, subalpine conifer forests, domain with *Picea* and blueberry, subalpine moor with acidic soil, mossy floor, *M. Vust* s.n. (G 00295947); ibid., Canton des Grisons, Davos, 1850 m, conifer subalpine forest, domain with *Picea* and blueberry, *Picea* forest, mossy floor, *M. Vust* s.n. (G 00295948); ibid., Ausserferrera, subalpine conifer forests, *Pinus cembra* forest domain, 1650 m, *Picea* forest, calcareous rock, mossy, *M. Vust* s.n. (G 00295949). – Canada, British Columbia, Fraser River Basin, SW of western border of Mt Robson Provincial Park, N53°1' E119°13', 1000 m, June 1995, *B. Goffinet* 4282 (CONN); ibid., Kispiox River Drainage, N55°24' W127°48', 600 m, Sept. 2006, on mossy log in disturbed conifer forest, *T. Goward* 06-329c (UBC). – USA, Montana, Flathead County, Glacier National Park, N48°43' W113°46', 1097 m, *B. McCune* 26218 (OSC); ibid., Alaska, Lake and Peninsula County, Katmai National Park, N58°33' W155°48', 18 m, *K. Spickerman* 160 (OSC). – Russia, Moscow city, Novomoscovsky adm. distr., Valuevsky forest-park, 20 quart., N55°35' E37°22', May 2019, mixed forest, on mosses (on old fallen tree), *E.E. Muchnik* N2 (MHA); ibid., Smolensk region, Demidovsky distr., near v. Korevo, National Park 'Smolenskoye Poozerye', N55°24' E31°56', July 2019, mixed forest, on mosses on old fallen tree, *E.V. Tikhonova* N4 (MHA); ibid., Sakhalin District, Nevelsky, N46°3' W141°57', 30 m, *S. Tchabanenko* 3080 (SAKH); ibid., Khabarovsk Territory, Durminskoye forest-hunting area, c. 200 km south / southeast of Khabarovsk, North of Durmin Mt, Rovnyi Creek valley, N47°49' E135°57', 329 m, *J. Miadlikowska* s.n. (DUKE). – Japan, Hokkaido, Kitami Prov., Shari-Gun, Shiretoko National Park, N44°6' E145°6', 609 m, July 2010, *A. Frisch* 10 / Jp410 (UPS 522008); ibid., Hokkaido, Kitami Prov., Shari-gun, Shari-cho, Shiretoko National Park, along the trail from Iwaobetsu Onsen, Oldgrowth montane forest, N44°6' E145°6', 500–650 m, Aug. 2019, *N. Magain* DNA 8132 (LG).

Notes — In the absence of any reliable morphological characters for distinguishing between *P. vitikainenii* and two related species with neopolydactyla morphotype (*P. appalachiensis* and *P. neopolydactyla*), ITS is needed for a reliable identification. Chemistry, however, can be helpful in separating *P. vitikainenii* (zeorin, peltidactylin and sometimes dolichorrhizin present) from *P. neopolydactyla* (only zeorin present). Additionally, *P. appalachiensis* is more common in boreal North America, whereas *P. vitikainenii* occurs more frequently in boreal Europe and Asia. Moreover, *P. appalachiensis* has an emerald green thallus in boreal regions.

Magain et al. (2017b) distinguished two putative taxa within *P. vitikainenii*, referred to as *P. neopolydactyla* 2a and 2c. These

**Fig. 36** *Peltigera vitikainenii*. a. Holotype from Norway (*N. Magain & E. Timdal* P384, O), b. upper and c. lower surface from Norway (*N. Magain* P360, LG); d. from Switzerland (*M. Vust* s.n., G 00295949).

two lineages are treated here as a single species because: 1) they share identical ITS barcode (although COR1b and COR3 sequences are different); 2) they are similar morphologically and chemically; and 3) they are associated with the same *Nostoc* phylogroups. It is possible that these two lineages are undergoing incipient speciation as their geographic ranges are largely non-overlapping, i.e., *neopolydactyla* 2c is restricted to East Asia, whereas *neopolydactyla* 2a occurs also in North America and Europe where it is locally common.

*Peltigera vitikainenii* shares its *Nostoc* phylogroups with other species from the dolichorhizoid and scabrosoid clades such as *P. pacifica* and *P. nigriventris*, and from other sections (e.g., *Peltigera*), such as *P. degenii*.

In Europe, mostly in boreal forests of Scandinavia and most likely in neighboring areas, e.g., Russia and Baltic countries, three species with typical neopolydactyla morphotype occur: *P. appalachiensis*, *P. neopolydactyla* and *P. vitikainenii*. Vitikainen (1994a) reported several localities of *P. neopolydactyla* further south, in mountainous areas from the Black Forest in Germany to the Caucasus; our sampling from these areas is sparse but based on the ITS barcode the following represent *P. vitikainenii*: three collections from France (Cantal, Pyrenees and Vosges), four collections from Switzerland (Alps) and one collection from Ukraine (Carpathian Mountains). It is therefore possible that all reports of *P. neopolydactyla* south of the boreal regions belong to *P. vitikainenii* (Goffinet et al. 1994, Hafellner & Türk 2001, Wirth et al. 2013, Roux et al. 2014, Nimis et al. 2018). The ITS barcode of the collection from France (Western Pyrenees) included in Goffinet et al. (1994) clearly matches *P. vitikainenii*. One collection from Switzerland may represent *P. occidentalis* but we could not confirm this identification with good quality sequence data.

## 4. The *occidentalis* subclade

### ***Peltigera esslingeri*** Magain, Miadl. & Sérus., *sp. nov.* — MycoBank MB 845076; Fig. 37a–d

*Synonym*. *Peltigera* sp. 6 in Magain et al. (2017b).

*Etymology*. This species is dedicated to our colleague Ted Esslinger to acknowledge his contribution in the field of biodiversity and taxonomy of macrolichens (mainly in the *Parmeliaceae*).

*Typus*. Honduras. Francisco Morazan Dept, San Antonio de Oriente, on flank of Cerro Uyuca, N14°4’ W87°6’, 1400 m, May 1996, on bare soil of seeping cliff, *B. Allen* 17790 (holo TEFH; iso NY).

Reference sequence: KX897357.

*Thallus* rather large (5–10 cm across), lobes 5–8 mm wide, not fragile. *Upper surface* bluish gray or gray to dark brown when dry, becoming darker when wet, more or less plane to undulating or rarely scrobiculate, smooth, matt or slightly shiny; young lobes sometimes bearing a pruina of whitish crystals; lobe margins plane to slightly raised or more typically involute. *Vegetative propagules* not seen. *Lower surface* whitish to pale gray or orange brown, veins ochraceous near the margins, flat or slightly raised, with small rounded interstices, transitioning to dark brown or black with elliptical, distinctly contrastive interstices toward the thallus center. *Rhizines* sparse to abundant, scattered, up to 0.8–1 cm long, dark brown to black, simple or branched, fasciculate or sometimes forming flocculent masses. *Apothecia* rare, finger-shaped, 4–5 mm long, disc orange brown to dark reddish brown, margin denticulate when young. Mature ascospores not seen. *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup XIX (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (major to minor) and gyrophoric acid (trace); triterpenes: peltidactylin (minor), dolichorrhizin (major), zeorin (major) and accessory 2 and perhaps 5 (Fig. 15, S7).

Barcodes — ITS1 (TATGGGCTT)**CATAAC**(CCC), ITS1 (GGG)**CATACAAT**(ATATAT); ITS2 (TTAG-TG)**GCGATAAT** (GTAGA) (Fig. 9).

Ecology — On bare or mossy soil in mid elevations, in pristine and disturbed forests.

Distribution — Central and South America (Honduras, Panama, Jamaica, Colombia and Peru).

*Selected specimens examined*. Colombia, Cundinamarca, Chipaque, Vereda Marilandia, dirt road from the main road towards the sanctuary, 2400 m, Sept. 2011, *R. Lücking & B. Moncada* 33658, 33659 (DUKE, UDBC). – Jamaica, Portland Gap, Blue Mountains National Park, St. Thomas, right above Jacob’s Ladder on trail to Portland Gap, N18°3' W76°37', 1490 m, Apr. 2018, mixed forest: montane broad-leaf forest and disturbed (coffee plantations), on soil between moss, *J.A. Mercado-Díaz* 3343 with *M. Dal Forno* (F); ibid., St. Peter, St. Andrew, Cinchona Botanical Gardens, N18°4' W76°39', 1677 m, Apr. 2018, soil outcrop in montane broad-leaf forest, *J.A. Mercado-Díaz* 3591a with *M. Dal Forno* (F). – Panama, Chiriqui prov., Volcan Baru National Park, Sendero Volcan, N8°49' W82°34', 2336 m, July 2016, *N. Magain* NM49 (DUKE). – Peru, Departamento Puno, Provincia Carabaya, Distrito Ollachea, S13°43' W70°27', 2270 m, May 2012, *N. Magain* DNA-P1734 (DUKE).

Notes — In section *Polydactylon*, several other species with similar upper surface (*P. dolichorhiza*, *P. borinquensis*, *P. kukwae*) also occur in the mountains of Central America and adjacent regions of the northern Andes. However, *P. esslingeri* has a characteristic occidentalis-type lower surface with the veins markedly differing in the outer (pale orange) and inner (very dark) parts of the thallus. Another *Peltigera* species with an occidentalis-like lower surface (*P. truculenta*) occurs further south in South America (Argentina and Chile).

### ***Peltigera occidentalis*** (E. Dahl) Kristinsson, The Bryologist 71, 38. 1968 — MycoBank MB 345554; Fig. 6c, d, 38a, b

*Basionym*. *Leciophysma occidentale* E. Dahl, Medd Grønkand, Biosciences 150: 44. 1950.

*Etymology*. Unknown but ‘*occidentalis*’ means western.

*Typus*. Denmark, Greenland, Julianehaab District, Qordlortorssuaq, 1937, *E. Dahl* (holo O, n.v.).

Reference sequence: KX897276.

*Thallus* large 10–15(–30) cm across, robust and usually not brittle when dry; lobe margins typically involute, sometimes raised or flat. *Upper surface* flat or corrugate (with small narrowed folds; sensu Goward et al. 1995) or more often slightly undulating, smooth, matt; gray or bluish gray to gray brown when dry, typically emerald green when wet, except gray brown in SE USA populations. *Vegetative propagules* not seen. *Lower surface* pale orange to brownish near lobe margins with veins forming a dense network interlacing small interstices, with a brownish araneous hyphal layer covering them, veins almost flat, diffuse toward lobe margins, becoming black towards the thallus center where they form a distinct network with oval or less visible interstices. *Rhizines* rare or abundant, rather short (2–4 mm long) but sometimes much longer (up to 9 mm long), frequently fasciculate or bush-like, or forming flocculent/flaky masses, rarely simple. *Apothecia* frequent, finger-shaped, up to 6–8 mm long, disc reddish brown, with a denticulate margin. *Ascospores* filiform but not flexuose, almost cylindrical and getting thinner towards the ends, (5–)7-septate, 78–95 × 3–4 µm (n = 18). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: VIIa and VIIb (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (minor) and gyrophoric acid (trace); triterpenes: peltidactylin (major), dolichorrhizin (minor), zeorin (minor) and accessory 5 and perhaps 2 (Fig. 15, S7).

Barcodes — ITS1 (TATGGG)**CTTAATAAT**(CCCTAC), ITS1 (TGGTTTGCTTGGG)**CATATAATA**(TRTATA) and ITS2 (GGCAA) **AAGACG**(TGCTACCGGTTG) (Fig. 9).

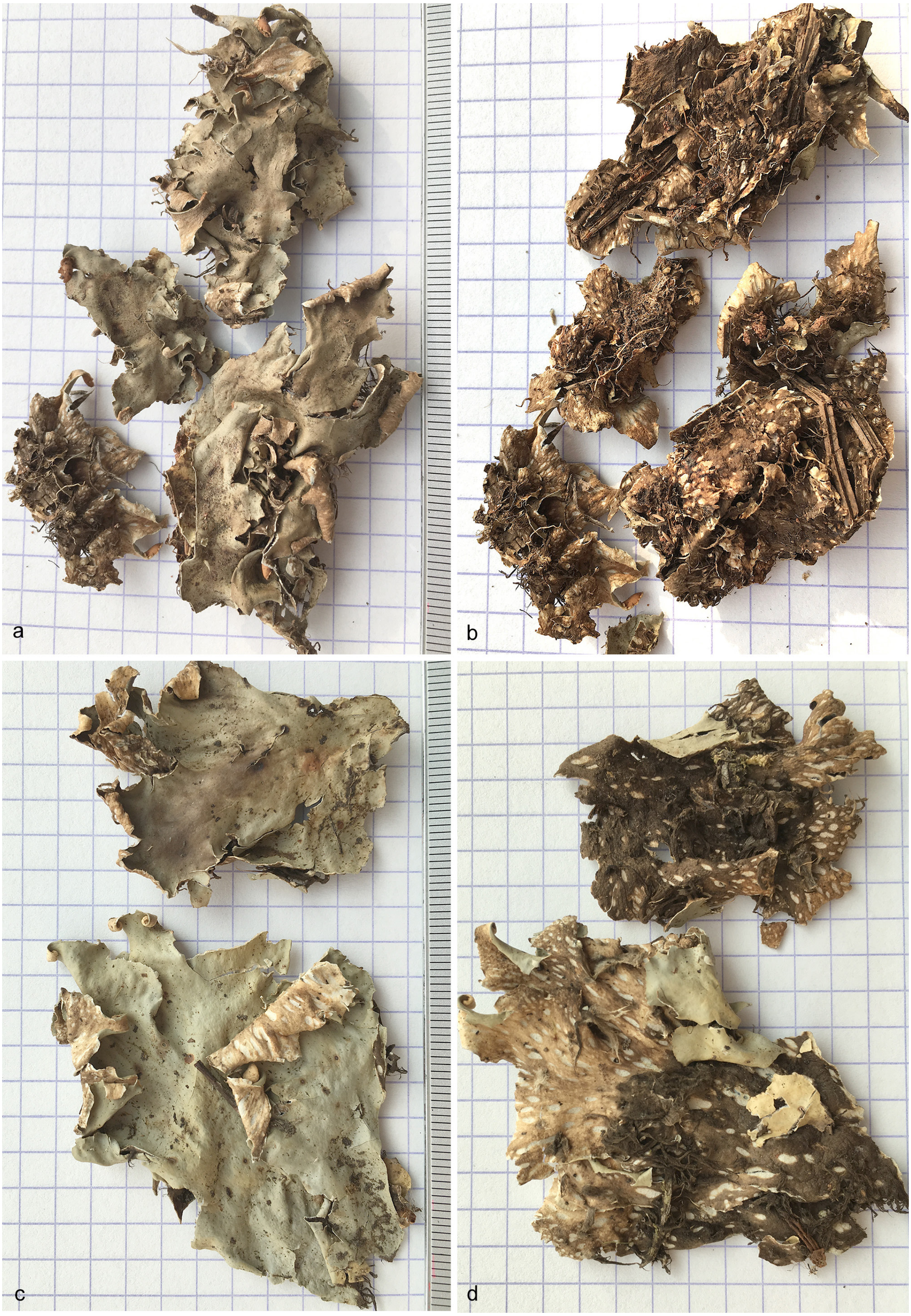

**Fig. 37** *Peltigera esslingeri*. a, b. Holotype from Honduras (*B. Allen* 17790, TEFH), a. upper and b. lower surface; c, d. from Colombia (*R. Lücking & B. Moncada* 33658, UDBC), c. upper and d. lower surface.

**Fig. 38** a, b. *Peltigera occidentalis*. a. From Norway (*S. Rui & E. Timdal* 9145, O); b. from Québec, Canada (*J. Miadlikowska & F. Lutzoni* P103, DUKE). — c, d. *Peltigera orientalis*. c. Holotype from Honshu, Japan (*E. Sérusiaux* DNA3304, TNF); d. close-up on the lower surface of the holotype.

Ecology — On mossy soil (in heaths or meadows) and rocks, sporadically on mossy logs, in forests or open habitats, especially where seasonally submerged in water.

Distribution — Widespread in the boreal regions of the northern hemisphere: Northern Europe (reported from Greenland, Svalbard, Finland, Norway and Sweden by Vitikainen 2007), Estonia; North America (Canada / British Columbia and Québec; USA / Alaska); and East Asia (Russia / Nenetsk, Tuva, Yakutia and Khabarovsk region); also found in temperate regions in SE USA (North Carolina, Tennessee).

*Selected specimens examined*. Norway, Nord-Trøndelag, Snasa, UM 677290, 25 m, June 2000, on lakeshore, *S. Rui* & *E. Timdal* 9145 (O); ibid., Uldalen, N61°49' E9°37', 800 m, Aug. 2011, conifer forest near river, *N. Magain* s.n. (LG); ibid., Gloppen, 20 km southeast of Sandone, N61°41' E6°27', 500 m, Aug. 2002, mossy rock on open granitic slopes, *T. Goward* 02-1468 with *J. Annonby* (UBC). – Estonia, Tartu county, Kastre commune, Järvselja looduskaitsekvartal, N58°17' E27°19', Sept. 2019, old drained peatland forest with spruce and pine, on mosses, on ground, *A. Animägi* (TUF088253). – Canada, Québec, Baie-James, Nord-du-Quebec, N52°25' W73°4', July 2011, *J. Miadlikowska* & *F. Lutzoni* DNA-P103 (DUKE); ibid., British Columbia, Clearwater Valley, Philip Lake Trail to Table Mountain, N51°51' W119°54', 1600 – 2200 m, Aug. 2009, on ground in subalpine spruce-fir forest to subalpine meadows, *J. Hollinger* 425 with *T. Goward* (UBC); ibid., west of Caribou Meadow, N51°53' W119°54', 1767 m, Aug. 2015, in oldgrowth forest at margin of small sylvan pool, over moss, *T. Goward* 15-64 with *C.R. Björk* (UBC). – USA, Alaska, Anchorage Co, Alaska Pacific University Campus Forest, N61°11' W149°48', 55 – 60 m, *T. Ahti* 63231 (H); ibid., North Carolina, Macon Co, Highlands, N35°3' W83°11', *R.C. Harris* 52559 (NY); ibid., Tennessee, Cocke Co, Great Smoky Mountains National Park, near top of Snakeden Trail, N35°44' W83°15', 1736 m, May 2011, on mossy *Betula* trunk in mossy birch forest high on north slopes, *J. Hollinger* 2844 (UBC). – Russia, Khabarovsk Territory, Bol'shekhetzkhirskii State Reserve, Polovinka sector, c. 48 km southwest of Khabarovsk, above the Polovinka Cabin at Polovinka Creek, N48°14' E134°54', 283 m, *J. Miadlikowska* & *F. Lutzoni* s.n. (DUKE); ibid., Tuva Republic, South Siberia Mountains, Todginskaya Valley, N52°23' E96°35', c. 950 m, *T.N. Otnyukova* (H); ibid., Nenets Autonomous Region, Western part of the Bolchezemeklskoy tundra, right bank of the Ortina River, forest island on the second terrace of an unnamed stream flowing into the Kainvozh stream, Aug. 1996, Elnik-green lingonberry, on mosses, *O.B. Lavrinenko* 127 (LE).

Notes — *Peltigera occidentalis* was introduced by Kristinsson (1968) and later recircumscribed by Vitikainen (1985). Despite its distinctive morphology this species was subsequently subsumed within *P. neopolydactyla* (Holtan-Hartwig 1993, Vitikainen 1994a). Its specific status was first re-established by Goward et al. (1995) and later confirmed by multiple phylogenetic and taxonomic studies (Miadlikowska & Lutzoni 2000, Vitikainen 2007).

When well developed, *P. occidentalis* is easily recognised by its robust habit and unique emerald green color when wet, in addition to its typical occidentalis morphotype. Some thalli, however, closely resemble *P. appalachiensis* which can also be emerald green and both species co-occur in boreal and alpine/arctic regions of the northern hemisphere. In such cases, the details of the lower surface are diagnostic: oval and regular interstices define *P. occidentalis* whereas variously shaped and irregular interstices are found in *P. appalachiensis*. This pattern, however, is not always very well visible and the ITS barcode is recommended for reliable identification. The same applies to the brown photomorphs of both species in the Appalachian Mountains in the USA.

### ***Peltigera orientalis*** Magain, Jüriado, Miadl. & Sérus., *sp. nov*. — MycoBank MB 845077; Fig. 38c, d

*Synonym*. *Peltigera* sp. 12 in Magain et al. (2017b).

*Etymology*. The epithet refers to Eastern Asia, the only region where this species is known so far.

*Typus*. Japan, Honshu, Kii Sanchi peninsula, SE of Koyasan, N34°11' E135°37', 750 m, Apr. 2013, disturbed forest by a small river, on mossy ground, *E. Sérusiaux* DNA3304 (holo TNS; iso LG).

Reference sequence: MF908496.

*Thallus* rather large (5 – 8 cm across), with lobes 5 – 10 mm wide, not fragile; lobe margins typically involute or plane to slightly raised. *Upper surface* undulating and locally strongly scrobiculate, smooth, matt or shiny, gray to dark brown when dry, becoming darker when wet. *Vegetative propagules* not seen. *Lower surface* whitish to pale gray or orange brown near lobe margins, veins ochraceous, flat or raised, extending to lobe edges where they surround small rounded interstices, veins become dark brown to black and form a distinct network with elliptical interstices toward the thallus center. *Rhizines* sparse, never abundant, scattered, up to 0.8 – 1 cm long, dark brown to black, simple or branched, fasciculate, not forming flocculent masses. *Apothecia* finger-shaped, 4 – 5 mm long, disc brown to dark reddish brown, margin denticulate when young. *Ascospores* filiform but not flexuose, almost cylindrical and becoming thinner towards the ends, 5 – 7-septate, 87 – 100 × 3 – 4 μm (n = 8). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup VIIb (Magain et al. 2017a, b).

Chemistry — Tenuiorin (major), methylgyrophorate (minor) and gyrophoric acid (trace); triterpenes: peltidactylin (minor), dolichorrhizin (major), zeorin (major) and accessory 2, 5, 6 and 11 (Fig. 16, S8).

Barcodes — ITS1 (TATGGGATT)**AATAACCCCTT**(ACGAA), ITS1 (TTGGG)**CATGAAA**(TATATA) and ITS2 (GGCT)**CCTTGC**(ATGG) (Fig. 9).

Ecology — On soil and mossy ground in disturbed forest.

Distribution — Currently known from Japan (Honshu).

*Selected specimens examined*. Japan, Honshu, Tochigi Prefecture, Nikko National Park, on shores of lakes Karikome and Kirikole, N36°49' E139°26', 1444 m, Oct. 2017, epigeic, on ground, *I. Jüriado* DNA 779 (TUF053893); ibid., 5.3 km ESE of Yumoto Onsen, the Utsunomiya University forest on the south slope of Mt. Taro, NE of where the dirt road ends, N36°48' E139°29', 1656 m, Sept. 2019, *D. Ertz* 24583 with *G. Thor*, *M. Grube*, *C. Printzen* and *B. Kanz* (BR).

Notes — All three specimens representing *P. orientalis* have the occidentalis morphotype but the rhizines are not bush-like and do not form flocculent / flaky masses. Both *Peltigera neopolydactyla* and *P. polydactylon* have been reported from Japan (Inumaru 1943, Kurokawa 2003: Checklist of Japanese Lichens, last update https://eng.lichenjapan.jp/: 09 / 03 / 2017, Kurokawa & Kashiwadani 2006) and Korea (Wei et al. 2009). It is possible that some of these reports represent *P. orientalis*. *Peltigera orientalis* was collected in Japan co-occurring with *P. mikado*, which is also common in China / Yunnan and Taiwan where *P. orientalis* may be present as well. *Peltigera occidentalis* was found in Khabarovsk (Eastern Russia), so its presence in Japan is possible, although probably in more northern localities compared to *P. orientalis*.

## 5. The *scabrosella* subclade

### ***Peltigera flabellae*** Magain, Goward, Miadl. & Sérus., *sp. nov*. — MycoBank MB 845078; Fig. 39c, d

*Synonym*. *Peltigera* sp. 7a in Magain et al. (2017a, b).

*Etymology*. The name refers to the fan-like shape of the lobes, which is characteristic for this species.

*Typus*. Canada, British Columbia, N of Hazelton, N55°23' W127°49', (no elevation given), on mossy log, Oct. 1994, *T. Tønsberg* 20741 & *T. Goward* (holo UBC; iso BG).

Reference sequence: KX897364.

*Thallus* large (5 – 14 cm across) with multiple lobes arranged and shaped like a fan, each lobe being more or less stipitate, lobes large (2 – 3(– 4) cm wide), thin but not fragile; lobe margins plane to undulating, slightly enlarged, flat. *Upper surface*

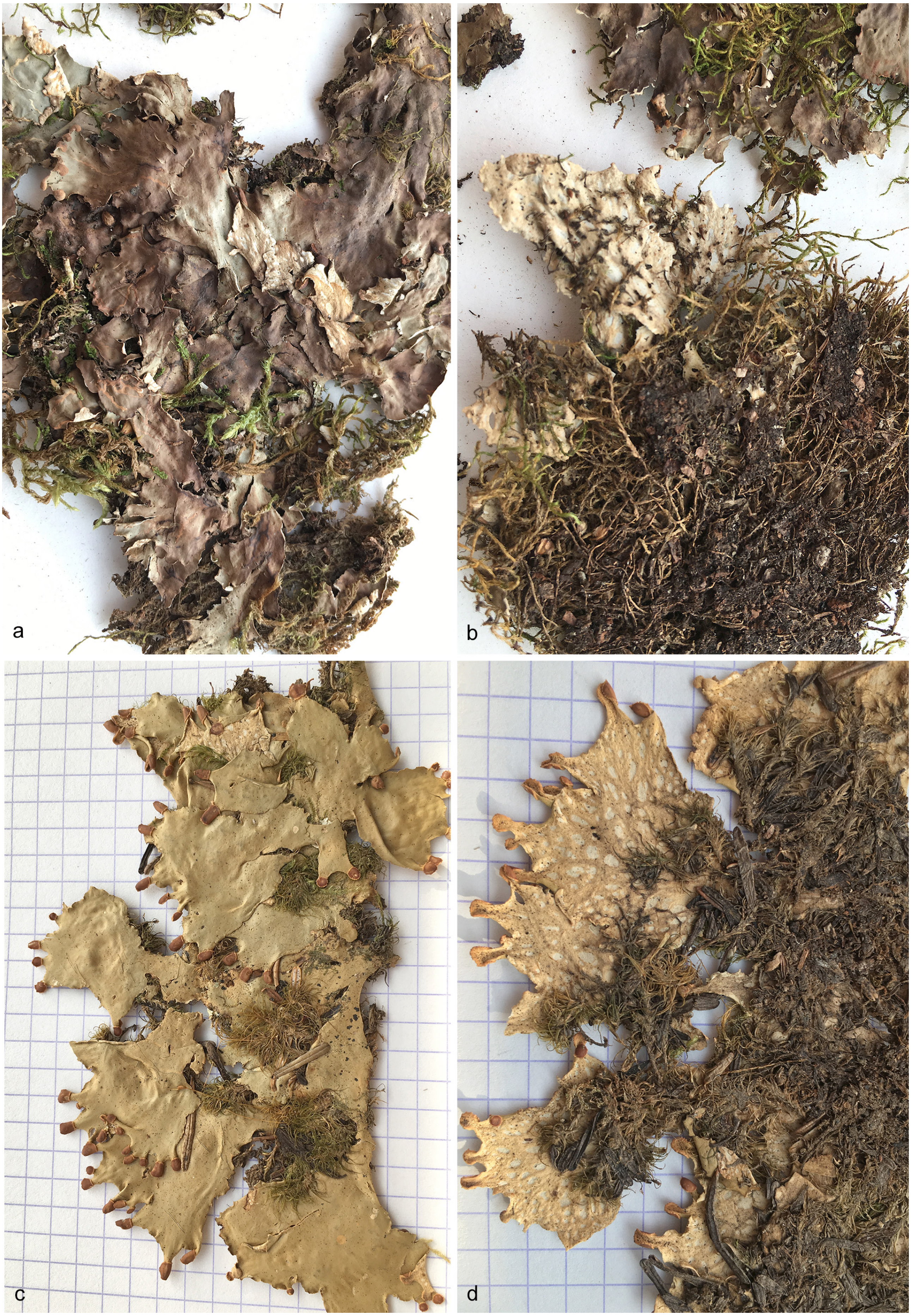

**Fig. 39** a, b. *Peltigera hokkaidoensis*, holotype (*G. Thor* 25401, TNF), a. upper and b. lower surface. — c, d. *Peltigera flabellae* from British Columbia, Canada (*T. Tønsberg* & *T. Goward* 20741, UBC), c. upper and d. lower surface.

plane to slightly undulating, smooth, matt or slightly shiny, greenish brown to pale or dark brown when dry, olive-colored, dark green to lead gray when wet. *Vegetative propagules* not seen. *Lower surface* whitish to pale ochre or orange, never dark (brown or black); veins orange to pale brown, 1–2 mm wide, slightly raised, forming a regular network around rather ellipsoid to almost circular interstices which extends to the lobe tips. *Rhizines* sparse and scattered, 5–8 mm long, pale brown to dark brown or almost black, simple to fasciculate. *Apothecia* rare, but often abundant when present, growing on short lobes in a regular arrangement along the lobe tips (resembling the fingers of an open hand), disc flat to slightly convex when young and becoming finger-shaped when mature, light brown to reddish brown when young, with a denticulate margin. *Ascospores* filiform, almost cylindrical, hardly flexuose, 7-septate, 88–120 × 3–4 µm (n = 10). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup XIa (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (minor) and gyrophoric acid (trace); triterpenes: no peltidactylin, dolichorrhizin (minor to trace), zeorin (major) and accessory 2, 6, 13, 15 and perhaps 3 (Fig. 16, S8).

Barcodes — ITS1 (CTACC)**TACATTA**(AAATT) (Fig. 9).

Ecology — On mossy logs in very humid forests.

Distribution — Currently known from Canada/British Columbia in western North America.

*Selected specimens examined*. Canada, British Columbia, same locality and date as type, *T. Tønsberg* 20742 & *T. Goward* (BG); ibid., Vancouver Is., Pacific Rim Hwy, N49° W124°30', Nov. 1992, along stream, *B. Goffinet* 2167 (CONN); ibid., Mount Arrowsmith, N49°14' W124°36', 1000 m, Oct. 2006, over moss, in subalpine krummholz, *T. Goward* 06-1256 (UBC); ibid., Whistler area, N of town up 16 Mile Creek, N50°10' W122°56', 800 m, Oct. 2006, mossy log in oldgrowth forest, *T. Goward* 06-1365, 06-1368 and 06-1371 (UBC); ibid., Coast Ranges, Bute Inlet, North Orford Valley, 930 m, Sept. 2009, mossy bank by creek, *C.R. Björk* 19542 (UBC).

Notes — *Peltigera flabellae* is a rare species easy to recognise by its fan-like greenish brown thallus (when dry), flat to sligthly convex, pale brown when young apothecia, which are arranged along lobe tips like the fingers of an open hand. Its pale lower surface (veins and interstices) throughout the thallus resembles *P. scabrosella*; however, its rhizines tend to be dark brown. Specimens referred to this species were identified as *P. neopolydactyla*, which is an unrelated species in the scabrosoid clade (Fig. 1, 3). So far, *P. flabellae* is restricted to Canada (British Columbia).

*Peltigera flabellae* shares its *Nostoc* phylogroup with its two closest relatives (*P. scabrosella* and *P. hokkaidoensis*) and two species from the scabrosoid clade (*P. neopolydactyla* s.str. and *P. scabrosa* s.str.) (Magain et al. 2017a).

### *Peltigera hokkaidoensis* Magain, Miadl. & Sérus., *sp. nov.* — MycoBank MB 845079; Fig. 32b, 39a, b

*Synonym*. *Peltigera* sp. 7b in Magain et al. (2017a, b).

*Etymology*. The epithet refers to the island of Hokkaido, Japan, where this species was first discovered.

*Typus*. Japan, Hokkaido, Kitami prov., Shiretoko National Park, c. 10 km NE Utoro town, N44°5' E145°7', 1198 m, July 2010, oldgrowth subalpine forest dominated by *Betula ermanii*, on *Alnus maximowiczii*, *G. Thor* 25401 (holo TNS; iso UPS).

Reference sequence: KX897367.

*Thallus* 5–8 cm across, with lobes 1–1.5 cm wide, not fragile; lobe margins plane or slightly involute. *Upper surface* shallow and undulating with large depressions, smooth, matt or slightly shiny; grayish to dark brown when dry, becoming dark green when wet. *Vegetative propagules* not seen. *Lower surface* whitish to pale orange brown, with veins slightly raised, 1–2 mm wide, orange at the margins, usually becoming dark brown towards the thallus center, forming a regular network around the rather ellipsoid interstices which extends to lobe margins. *Rhizines* sparse and scattered, 2–6 mm long, dark brown to black, simple to fasciculate, rarely fibrillose. *Apothecia* rare, developing directly on main lobe margins or situated on small lobes outgrowing from the main lobe margins, disc convex, orange brown to dark reddish brown, almost rounded, with a slightly denticulate margin. *Ascospores* filiform, almost cylindrical, hardly flexuose, 7-septate, 90–121 × 3–4 µm (n = 18). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup XIa (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (minor) and gyrophoric acid (trace); triterpenes: peltidactylin or unknown (trace), perhaps dolichorrhizin, zeorin (major) and accessory 2, 6, 12 and 15 (Fig. 16, S8).

Barcodes — ITS1 (CACA)**AGAAAGC**(ATCGG), ITS1 (TACC) **AACATTA**(AAATT) (Fig. 9).

Ecology — Mostly epiphytic, often at the base of coniferous tree trunks in subalpine forests, but also on mossy rocks.

Distribution — Japan/Hokkaido and Honshu.

*Selected specimens examined*. Japan, Hokkaido, same locality as type collection, *G. Thor* 25408 (UPS); ibid., Nakagawa-gun, Bifuka, Niupu, on the summit of Mt. Hakodake, N44°40' E142°25', 1100 m, Aug. 2019, *N. Magain* 8029 with *A. Simon*, *E. Sérusiaux*, *C. Partoune* (LG); ibid., Nakagawa-gun, Nakagawa, summit of Mt. Panke, N44°52' E142°9', 600 m, Aug. 2019, slope with bamboo shoots and rocks, *N. Magain et al.* 8022 (LG); ibid., Urakawa-gun, Urakawa, on the trail towards Mt. Petegari starting from Petegari Sanso, N42°29' E142°52', 1000 m, Aug. 2019, *N. Magain et al.* 8117, 8135 (LG); ibid., Honshu, Fukushima Prefecture, Yama District, Kitashiobara, Hibara, beyond the ski slope at Grandeco Snow Resort towards Mt. Nishi-Agatsuma, N37°44' E140°8', 1730 m, Aug. 2019, on *Tsuga*, in subalpine conifer forest, *A. Simon* 676, 677 with *E. Sérusiaux* (LG).

Notes — Currently *P. hokkaidoensis* is known only from Japan: several localities in Hokkaido and one in Honshu. Morphologically, it resembles *P. polydactylon*, however, its venation is less dense especially toward the lobe margins, and its lower surface as a whole is usually paler. Earlier reports of *Peltigera* from Hokkaido (e.g., Kashiwadani & Inoue 1993, Ohmura & Kashiwadani 1997, Shiba et al. 2008) may include *P. hokkaidoensis*. As recently redelimited (Magain et al. 2017b), *P. dolichorhiza* is not present in Japan, whereas the status of *P. polydactylon* subsp. *udeghe* (present in Hokkaido and Honshu; Magain et. al. unpubl.), and in other parts of East Asia needs further study (Magain et al. 2016).

*Peltigera hokkaidoensis* shares its *Nostoc* symbiont with the two closest relatives (*P. scabrosella* and *P. flabellae*) and with two species from the scabrosoid clade (*P. neopolydactyla* s.str. and *P. scabrosa* s.str.) (Magain et al. 2017a).

### *Peltigera scabrosella* Holt.-Hartw., The Lichenologist 20: 15. 1988 — MycoBank MB 132385; Fig. 40a–e

*Etymology*. The epithet refers to the scabrous upper thallus surface, the morphological feature shared with *P. scabrosa*.

*Typus*. Norway. Nord-Trøndelag, Grong, Sanddøldalen, Hansmoen, 230 m, Sept. 1981, *J. Holtan-Hartwig* 1655 (holo O, n.v.).

Reference sequence: KX897332.

*Thallus* usually small (2–3 cm across), sometimes larger, usually strongly attached to the substrate, with imbricate, narrow lobes usually less than 1 cm wide, sometimes forming small fan-like lobes, not fragile; lobe margins ascending and undulating. *Upper surface* not undulating, scabrous, at least at lobe margins, matt; grayish to gray brown, rarely dark gray when dry, darker when wet. *Vegetative propagules* not seen. *Lower surface* whitish to pale orange throughout, veins slightly raised, pale orange, forming an indistinct network around the

**Fig. 40** a–e. *Peltigera scabrosella* from Norway; a, b. *J.T. Klepsland* JK09-L224 (O), a. upper and b. lower surface; c. *E. Timdal* 9486 (O); d, e. *N. Magain* DNA-P514, LG, d. upper and e. lower surface of thallus.

interstices. *Rhizines* abundant and becoming aggregated into intricate flabby mats, otherwise simple and slender, pale or brownish. *Apothecia* rare, plane or convex, rounded to slightly elongated, developing on short elongated lobes or rarely on the main lobes, disc reddish brown. *Ascospores* filiform, almost cylindrical, hardly flexuose, 7-septate, 94–110 × 3–4 µm (n = 20). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup XIa (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (minor) and gyrophoric acid (trace); triterpenes: no peltidactylin, dolichorrhizin (minor), zeorin (major) and accessory 2, 4, 5, 6 and 13 (Fig. 16, S8).

Barcodes — ITS1 (AAAAAA)**GCATCGGGTTGCCCAGAAGACTACCTA**(AATTAAAA) (Fig. 9).

Ecology — On steep, seepy rocks in coastal regions, and on soil in alpine habitats, mainly in places with prolonged snow beds.

Distribution — Northern Europe, Greenland and north-western North America where it is apparently rare (Goward et al. 1995).

*Selected specimens examined*. Greenland, SW Greenland, Fiskenaesset, N63°6' W50°40', *E.S. Hansen* (H). – Norway, Enebakk, Nordskauen, N59°47' E11°8', 200 m, 2011, *N. Magain* s.n. (LG); ibid., Opland, Uldalen, N61°49' E9°37', 800 m, 2011, conifer forest near river, *N. Magain* DNA-P524, (LG); ibid., Trøndelag, Steinkjer, N63°58' E12°7', 480 m, 2011, conifer forest near river, *N. Magain* DNA-P514 (LG); ibid., Troms, Torsken, Senja, N69°17' E17°11', 10 m, July 2010, over mosses on vertical face of giant boulder in NW-facing scree, *T. Tonsberg* 40401 (BG L-89357); ibid., NNE of Balleskiva, N69°24' E17°8', 20–30 m, July 2010, on mossy, N-facing wall of giant boulder in boulder field in *Betula pubescens* forest, *T. Tonsberg* 40482 (BG L-89430); ibid., Telemark, Seljord, Grisejuvet, 200–300 m, July 1996, on rock wall near stream in bottom of canyon, *H. Bratli* & *E. Timdal* 8410 (O L22626); ibid., Buskerud, Sigdal, N60°19' E9°18', 1020 m, Sept. 2013, on rock wall in subalpine birch forest, S. *Rui* & *E. Timdal* 13200 (O L184740); ibid., Oppland, Lom, Boverdalen, N61°35' E8°2', 1180 m, Aug. 1989, among mosses on moist rock in the low alpine zone, *J. Holtan-Hartwig* & *E. Timdal* H1253 (O 18285); ibid., Nord-Trondelag, Snasa, Koltjonna, 200 m, Sept. 1981, *J. Holtan-Hartwig* 1663 (O L52922); ibid., Oslo, Sorkedalen, May 1980, *E. Timdal* s.n. (O L52448); ibid., Finnmark, Sor-Varkanger, N69°42' E30°29', 30 m, July 1986, *E. Timdal* 4602 (O L103013); ibid., Aust-Agder, Bygland, Lirasen, 500 m, Mar. 2002, *J.T. Klepsland* s.n. (O L133911); ibid., Vest-Agder, Farsund, Lista, June 1980, *J. Holtan-Hartwig* 223 (O L52497); ibid., Nordland, Hamaroy, Svartvasselva, 70 m, July 2009, *J.T. Klepsland* JK09-L224 (O L164759); ibid., Sor-Trondelag, Orksdal, Oct. 1997, on rock wall in N-facing old spruce forest, *S. Rui & E. Timdal* 8911 (O L27200); ibid., Hedmark, Tynset, Gammeldalen, Kloktet, N62°16' E11°00', 750 m, *R. Haugan*, *A. Often*, *E. Timdal* H1813 (O L5517); ibid., More Og Romsdal, Ulstein, Hareidlandet, June 1981, *J. Holtan-Hartwig* 690 (O L52914).

Notes — *Peltigera scabrosella* is easily recognised by its small size, scabrous upper surface and pale lower surface with flabby mats of rhizines; moreover, it thrives in highly specific habitats (mossy subvertical rocks in wet environments and snow beds in alpine conditions). It can be confused with *P. rangiferina*, which has a less scabrous upper surface and less distinct veins. The ITS barcode sequence confirmed the identity of 20 specimens (deposited in Oslo herbarium) collected in Norway and identified as *P. scabrosella* by Holtan-Hartwig (1993).

The GBIF portal (https://www.gbif.org/species/3423831; accessed on 3 Sept. 2017) includes records of *P. scabrosella* from Russia/Kola Peninsula, Norway, Finland, Svalbard, UK/Scotland, Iceland and Greenland. A single collection is mentioned by Goward et al. (1995) from Canada/British Columbia and another one from East Russia/Magadan region of the Okhotsk Sea (Zheludeva 2017), but no ITS data are available to confirm these records. Vitikainen (2007) also mentioned its occurrence in Asia, without providing further details. The exact distribution of *P. scabrosella* requires further investigation; so far, it has been confirmed only from Greenland and Norway.

## 6. The *melanorrhiza* subclade

***Peltigera chabanenkoae*** Magain, Miadl. & Sérus., *sp. nov*. — MycoBank MB 845082; Fig. 32a, 41a, b

*Synonym*. *Peltigera neopolydactyla* 7 in Magain et al. (2017b).

*Etymology*. In memoriam to Svetlana I. Chabanenko (1954–2018), our collaborator, an accomplished lichenologist and Deputy Director of Research in the Sakhalin Botanical Garden in Russia. We acknowledge her contribution to unravel lichen biodiversity in Russian Far East. She provided the type specimen of this species.

*Typus*. Russia, Sakhalin District, Iturup Is., N44°46' E147°11', 58 m, Aug. 2011, coniferous forest with *Abies sachalinensis* and *Picea yesoensis*, on mossy soil, *S. Chabanenko* 39 (holo SAKH-3072).

Reference sequence: MF908504.

*Thallus* medium-sized (4–6 cm across), robust; lobe margins plane. *Upper surface* undulating with large and irregular or sometimes inconspicuous depressions, smooth, matt or slightly shiny, greenish grey to brown when dry, with more vivid colors and usually dark bluish grey when wet. *Vegetative propagules* not seen. *Lower surface* whitish to pale orange brown near lobe margins, with indistinct veins obscured by an orange-brownish araneous hyphal layer, becoming dark brown to black toward the thallus center, diffuse, slightly raised, with distinct elliptical interstices. *Rhizines* sparse to abundant, mostly fasciculate, scattered or rarely aggregated, black, up to 1–1.4 mm long. *Apothecia* finger-shaped, 5–6 mm long, disc reddish brown, margin denticulate when young. *Ascospores* filiform and flexuose, almost cylindrical, 5–7-septate, 68–84 × 3–3.5(–4) µm (n = 14). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup XVII (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (major to minor) and gyrophoric acid (trace); triterpenes: peltidactylin (major), dolichorrhizin and zeorin absent or hardly detected and accessory 10 and two others that could be 5 and 6 (Fig. 16, S8).

Barcodes — ITS1 (TTAT)**CGAGGA**(CATGT), ITS1 (ATGG)**CTGTAA**(GCTAA), ITS1 (CTCC)**CCCCTCT**(CTAA) (Fig. 9).

Ecology — On mossy soil and stones in coniferous forests.

Distribution — Russia Far East, on Sakhalin Island; Japan, Hokkaido and Honshu.

*Other specimens examined*. Japan, Honshu, Tochigi prefecture, Nikko National Park, on shores of lakes Karikome, N36°49' E139°26', 1429 m, Oct. 2017, epiphytic on mossy stone, *I. Jüriado* DNA 777 (TUF053896); ibid., Hokkaido, Urakawa, Urakawa-gun, on the trail between Petegari Sanso and Kamui Sanso, Aug. 2019, *N. Magain et al.* 8098 (LG).

Notes — In boreal forests, *P. chabanenkoae* can be confused with *P. occidentalis* because of the similarities in their lower surface; however, when growing in similar habitats, *P. occidentalis* can have emerald green thalli when wet. The ITS barcode is recommended for a reliable identification of *P. chabanenkoae*. Its *Nostoc* is shared with *P. nigriventris* and *P. vitikainenii* (Magain et al. 2017a).

***Peltigera melanorrhiza*** Purvis, P. James & Vitik., Arquipélago, Cienc. Biol. Marin. 11A: 9. 1993 — MycoBank MB 361789; Fig. 30c, d, 42a

*Etymology*. This species, endemic to the Azores archipelago was named after its black rhizines and veins, a diagnostic feature of this species.

*Typus*. Portugal, Azores archipelago, Pico, Cerrado de Sonicas, c. 200 m along track off road EN3 to aerial, 900 m, 1992, *W. Purvis* & *P.W. James* s.n. (holo AZU; iso BM!).

Reference sequence: KX897210.

*Thallus* large (5–15 cm across) forming large, rounded rosettes on trunks or extensively overgrowing mosses on branches and

**Fig. 41** a, b. *Peltigera chabanenkoae*, holotype from Sakhalin, Russia (*S. Chabanenko* 39, SAKH), a. upper and b. lower surface. — c, d. *Peltigera clathrata*, holotype from Oregon, USA (*B. McCune* 26873, OSC), c. upper and d. lower surface.

**Fig. 42** a. *Peltigera melanorrhiza* from Azores (*E. Sérusiaux* DNA261, LG). — b–e *Peltigera borealis*. b, c. Holotype from Québec, Canada (*J. Miadlikowska* & *F. Lutzoni*, 08.07. 2011-SN6W3 P311, QFA); d. from Norway (*N. Magain* DNA-P533, LG), lower surface; e. from Tirol, Austria (*K. Kalb* 7178, DUKE).

twigs, lobes 1–2(–2.5) cm wide, rounded and overlapping, rather fragile. *Upper surface* smooth, matt to shiny, flat or slightly undulating, rarely scrobiculate, brownish to grayish when dry and typically dark lead blue when wet. *Vegetative propagules* in form of *phyllidia* rarely produced at lobe edges. *Lower surface* typically whitish to pale orange, with diffuse, flat and usually dark to almost black veins forming a dense irregular network with whitish interstices. *Rhizines* sparse to rarely abundant, simple to typically fasciculate, sometimes fibrillose, typically dark, 1–3 mm long. *Apothecia* usually frequent, developing on lobes extensions, slightly but clearly convex, 2–3 mm long, c. 1.5–2 mm large, disc pale reddish orange to brown, with a typically denticulate margin. *Ascospores* filiform and flexuose, almost cylindrical, 5–7-septate, 62–90 × 3–3.5(–4) µm (n = 18). *Pycnidia* not found.

Photobiont — *Nostoc* phylogroup XVI (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin absent, dolichorrhizin (major), zeorin (minor to trace) and accessory 2, 4 and 17 (Fig. 16, S9).

Barcodes — ITS1 (TGAGGGT)**ATTGTAG**(GCTAA), ITS1 (GGGC)**ACGGC**(TGTA), ITS1 (AGACCATG)**GCCCCTTATAA** (GGAAAA) (Fig. 9).

Ecology — On mossy trunks and branches, sometimes twigs, on native trees, or on mossy lava boulders, in pristine or disturbed stands of the laurisilva, at 600–900 m elev.

Distribution — Currently known from Faial, Pico and San Miguel in the Azores archipelago.

*Selected specimens examined*. Portugal, Azores, Pico, road to Pico da Urze, coming from road R3-2 ('longitudinal'), N38°29' W28°21', 800–810 m, Oct. 2007, disturbed cloud forest with *Juniperus brevifolia* and *Erica azorica*, on trees and mossy lava blocks, *E. Sérusiaux* 261 (LG); ibid., near Pico Caveiro, N38°26' W28°13', 760 m, Oct. 2007, very wet stand of cloud forest with large surfaces covered with *Sphagnum* and *Polytrichum*, *E. Sérusiaux* 289 (LG); ibid., *P. Divakar* 6918b (MAF).

Notes — *Peltigera melanorrhiza* is endemic to the Azores, where it is easily distinguished from other *Peltigera* species by its lower surface with black, flat diffuse veins extensively spreading and delimiting white interstices. It frequently cooccurs with another endemic taxon, *P. hymenina* var. *dissecta* (see description above), which is easily recognised by its fragile pale bluish to almost white thalli (when wet) and abundant marginal phyllidia. *Peltigera melanorrhiza* has also been reported from a single locality in Spain (Martínez & Burgaz 1997, Spain, Cáceres, Acebo, Sierra de Gata, 3 Apr. 1996, *G. Aragón et al.* 1175, MA!); however, the ITS barcode matches *P. hymenina*, a widespread species in Western Europe.

According to Aptroot et al. (2010), 10 other species of lichens are endemic to the Azores including two cyanolichens from the genus *Nephroma* (Sérusiaux et al. 2011).

Other species associated with *Nostoc* phylogroup XVI include closely related *P. nigriventris*, phylogenetically unrelated *P. hymenina* (from the dolichorhizoid clade), and species from other sections such as *P. membranacea* (*Peltigera*) and *P. britannica* (*Peltidea*) (Magain et al. 2017a).

***Peltigera nigriventris*** Magain, Goward, Miadl. & Sérus., *sp. nov*. — MycoBank MB 845086; Fig. 43a–d

*Synonym*. *Peltigera neopolydactyla* 6 in Magain et al. (2017b).

*Etymology*. The epithet refers to the blackish color of the veins on the lower surface of the thallus.

*Typus*. USA, Oregon, east of Port Orford, Grassy Knob Wilderness Area, N42°45' W124°22', 710 m, June 1998, *Lithocarpus*-*Pseudotsuga*-*Quercus* forest, on rock in roadcut, *B. McCune* 24160 (holo OSC).

Reference sequence: KX897264.

*Thallus* large (4–10 cm across) forming regular rosettes with rounded often quite large (up to 2–3 cm wide) lobes, robust and not fragile; lobe margins plane or slightly raised. *Upper surface* undulating with large and irregular depressions, smooth, matt or slightly shiny; greenish grey to brown, sometimes quite dark brown when dry, with more vivid colors and usually dark bluish grey when wet. *Vegetative propagules* not seen. *Lower surface* whitish to pale orange brown near margins, with hardly visible veins and sometimes with an orange-brownish araneous top layer, strongly darkening toward thallus center but always with distinct elliptical interstices (3–4 × c. 2 mm long when well-developed). *Rhizines* sparse to abundant, simple to mostly fasciculate, scattered or rarely aggregated, black and up to 1–1.4 mm long. *Apothecia* and pycnidia not seen (though apothecial initials sometimes present).

Photobiont — *Nostoc* phylogroups XIII and XVII (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (major), dolichorrhizin (major), zeorin (major) and accessory 2, 5 and 10 (Fig. 16, S9).

Barcodes — ITS1 (GAGG)**GTATGT**(GGGC), ITS1 (CCCC) **CCTTTATA**(AGGA) (Fig. 9).

Ecology — On mossy roadcuts and on logs in slightly disturbed humid forests, mostly at low elevations.

Distribution — Northwest North America: USA/Oregon and Canada/British Columbia.

*Selected specimens examined*. Canada, British Columbia, Vancouver Is., West coast, S. of Ucluelet c. N49° W125°, 1 m, Nov. 1992, *B. Goffinet* 3147 (CONN); ibid., Coastal British Columbia, south of Prince Ruppert, Port Edward, N54°25' W130°18', 15 m, Aug. 1990, *B. Goffinet* 414 (CONN); ibid., Loughborough Inlet, N50°40' W125°29', sea level, Aug. 2008, shoreline rock above estuary, *C.R. Björk* 17289 (UBC). – USA, Oregon, Rock Creek Wilderness, near Rock Creek, N44°11' W124°6', 10 m, Dec. 1993, *Picea sitchensis* and *Alnus rubra* forests, within 2 km of ocean, *B. McCune* 21501 (OSC); ibid., Curry Co., Humbug Mountain trail, N42°41' W124°26', 300 m, Sept. 2010, on shaded ground in old growth maritime forest, *J. Hollinger* 1386 (UBC); ibid., Coos Co, c. 13 km SW of Coos Bay, Sunset Bay State Park, N43°20' W124°22', sea level, Aug. 2000, *B. Goffinet* 8049 (CONN).

Notes — *Peltigera nigriventris* is endemic to humid areas of northwestern North America, where it can be identified by its robust neopolydactyla morphotype thalli with conspicuous, very dark and rather broad veins offset by large, conspicuous interstices. Such a contrasting pattern on the lower surface can also be present in other species of the neopolydactyla morphotype in the region, e.g., *P. appalachiensis*, *P. clathrata* and *P. vitikainenii*. The ITS barcode is therefore strongly recommended for a reliable identification.

The two *Nostoc* phylogroups associated with *P. nigriventris* are also present in *P. pacifica*, *P. vitikainenii*, and two members from section *Peltigera*: *P. membranacea* and *P. degenii*. Additionally, phylogroup XVII associates with *P. chabanenkoae* (Magain et al. 2017a, b).

## 7. The *scabrosa* subclade

***Peltigera borealis*** Magain, Miadl. & Sérus., *sp. nov*. — MycoBank MB 845087; Fig. 42b–e

*Synonym*. *Peltigera scabrosa* 1 in Magain et al. (2017a, b).

*Etymology*. The name was chosen to acknowledge a widespread occurrence of this species in boreal habitats of the northern hemisphere.

*Typus*. Canada, Québec, transect site SN6W3, N3°48' W 3°4', 374 m, July 2011, *Picea mariana* boreal forest, on mosses, *J. Miadlikowska* & *F. Lutzoni*, 08.07.2011-SN6W3, P0311 (holo QFA; iso DUKE).

Reference sequence: KX897305.

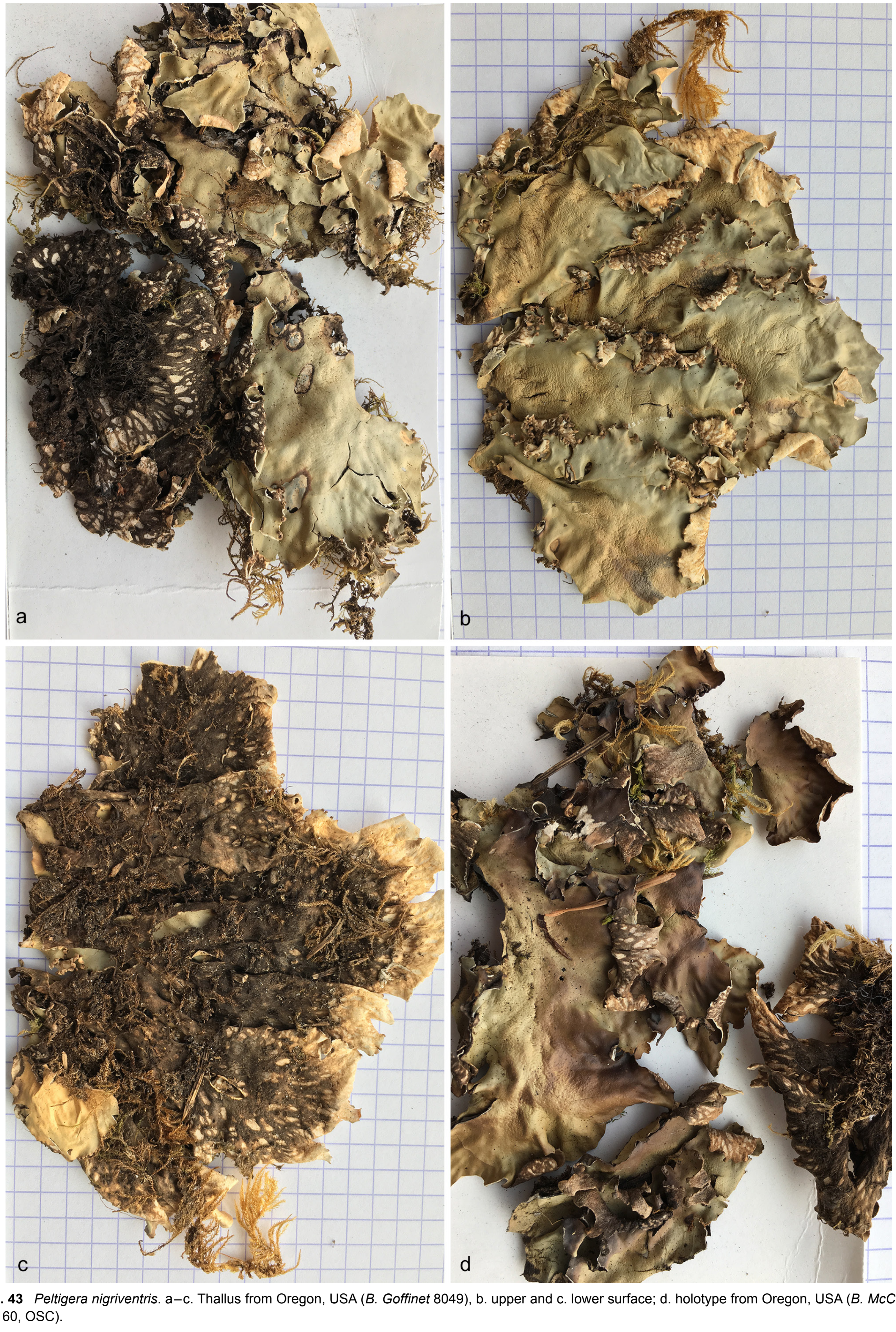

**Fig. 43** *Peltigera nigriventris*. a–c. Thallus from Oregon, USA (*B. Goffinet* 8049), b. upper and c. lower surface; d. holotype from Oregon, USA (*B. McCune* 24160, OSC).

*Thallus* usually conspicuous and large (up to 10–20 cm diam), usually forming regular rosettes, with large rounded lobes (up to 1–2 cm broad), robust but easily broken when dry; lobe margins plane or slightly raised. *Upper surface* undulating with inconspicuous depressions, typically scabrous, especially towards the lobe margins; grayish to brown when dry, vivid or emerald green when wet. *Vegetative propagules* not seen. *Lower surface* pale, almost white near lobe margins, veins raised or flat, pale brown or orange near lobe margins becoming much darker towards the thallus center, interstices not well visible. *Rhizines* sparse to usually locally abundant, fasciculate or brush-like, sometimes forming large mats, covering extensive parts of the lower surface. *Apothecia* rare and usually few, finger-shaped, margin hardly denticulate, 4–6 mm long, disc dark reddish brown to almost black. *Ascospores* filiform and flexuose, almost cylindrical and getting thinner towards the ends, 7–9-septate, 83–92(–104) × 3–4 µm (n = 23). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup VIIa (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: zeorin (major), peltidactylin and dolichorrhizin absent, accessory 11 (to be confirmed; could be 19) and perhaps 2 (Fig. 17, S9).

Barcodes — ITS1 (AGAC)**CATCTC**(CCTT) (Fig. 9).

Ecology — On ground or mosses in boreal or high altitude forests.

Distribution — North America: Canada / Québec and Alberta, Europe: Austria, Norway, Asia: Russia / Krasnoyarsk and Komi.

*Selected specimens examined*. CANADA, Québec, Baie-James, Nord-du-Québec, N47°55' W72°58', 374 m, boreal forest with *Picea mariana*, on thick pillow of mosses on ground, July 2011, *Arnold et al.* SN6-W3-2, (DUKE-0329898); ibid., Manicouagan County, Côte-Nord, N51°7' W68°31', 365 m, boreal forest with *Picea mariana*, on mossy ground, July 2011, *Arnold* & *Lutzoni* EW0-C1-2 (DUKE-0329773); ibid., Alberta, north side of Hwy. 40 southeast of Grande Cache, N53°36' W118°5', 1400 m, June 2009, on ground in dry, open boreal forest, *J. Hollinger* 1066 (UBC). – AUSTRIA, Tirol, Otztaler Alpen, Leierstal N-Hang in Cladonietum alpestris, 2100 m, Sept. 1966, *K. Kalb* 7178 (DUKE). – NORWAY, Kongsvoll, Mt Knutshø, N62°18' E9°38', 1200 m, semi-open area with shrubs and a few trees, near creek, 2011, *N. Magain* s.n. (LG); ibid., Dragasoya, N62°58' E10°54', 375 m, 2011, conifer forest near creek, *N. Magain* DNA-P533 (LG). – RUSSIA, Krasnoyarsk Territory, Reserve 'Stolby', near Fortress rocks, N55°53' E92°46', 1774 ft (acc. 42 ft), wet boreal forest with *Abies sibirica*, *Picea obovata*, *Pinus siberica*, grasses, and *Rubus nigra*, on mossy boulder and mossy slope, June 2012, *F. Lutzoni* & *J. Miadlikowska* 06.2012-P1539 (DUKE); ibid., Komi Republic, Gorod Inta, Yugyd Va National Park, old growth *Larix-Picea-Betula* forest near the Orlinoe tourist camp, N65°25' E60°41', Sept. 2019, on mosses, *I. Jüriado* 496 (TUF088263).

Notes — No validly published epithet is available to accommodate this species. Amongst boreal species with a scabrous upper surface, *P. borealis* can be easily identified by the presence of zeorin as the only triterpene; other members with the scabrosa morphotype in the northern hemisphere (*P. holtanhartwigii*, *P. rangiferina* and *P. scabroa*) produce dolichorrhizin and (or) peltidactylin. Similar to *P. holtanhartwigii* and *P. rangiferina*, *P. borealis* has an emerald green thallus when wet (Magain et al. 2017a). The ITS barcode is recommended for reliable identification.

*Peltigera borealis* is widespread in boreal forests and associated habitats, as well as in arctic and subalpine zones of the northern hemisphere. Although apparently less abundant in Europe than *P. scabrosa*, *P. borealis* is much more widespread in eastern North America, especially at relatively southern latitudes; in the north, it is replaced by *P. scabrosa* (Lu et al. 2018). Molecular data suggest that in Europe, it is the only species with a scabrous thallus occurring south of the boreal zone, including a single validated record from the Alps in Austria.

***Peltigera clathrata*** Magain, Goward, Miadl. & Sérus., *sp. nov*. — MycoBank MB 845088 ; Fig. 41c, d, 44a

*Synonym*. *Peltigera neopolydactyla* 5 in Magain et al. (2017b).

*Etymology*. This epithet refers to the sharp contrast between the veins and the lower surface of the thallus revealing a latticed pattern.

*Typus*. USA, Oregon, Benton Co, lower part of Fitton Green County Park, N44°35' W123°22', 171 m, Mar. 2003, on soil on roadcut in savanna, *B. McCune* 26873 (holo OSC).

Reference sequence: KX897260.

*Thallus* large (4–12 cm across), forming rosettes with rounded lobes up to 2.5 cm wide, robust and not fragile; lobe margins plane or slightly involute. *Upper surface* undulating with large and irregular depressions, smooth, matt; greenish grey when dry, with more intense colors when wet. *Vegetative propagules* not seen. *Lower surface* whitish to pale orange near lobe margins, with clearly raised orange veins overlain by an orange-brownish araneous layer, vein strongly raised, becoming dark brown to black towards thallus center, interstices elliptical, up to c. 4 × 3 mm, distinctly contrastive with veins. *Rhizines* sparse to abundant, simple to mostly fasciculate, scattered, black, up to 1–2 mm long. *Apothecia* sparse but present on all thalli examined, digitate on lobes extensions, c. 5 × 2–3 mm, disk reddish dark brown, with a denticulate margin. No mature spores observed. *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup XIb (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (major), dolichorrhizin (major), zeorin (major) and accessory 2, 4, 11 and 18 (Fig. 17, S9).

Barcodes — ITS1 (GGGCAT)**GGGCTTG**(TAG)**GCTTAAAA**(GACT)**CAAGTTTA**(TCCT); each of the three barcodes is unique for this species (Fig. 9).

Ecology — On mossy rocks and logs in oldgrowth forests.

Distribution — Currently kown from northwestern North America: USA / Oregon and Canada / British Columbia.

*Selected specimens examined*. CANADA, British Columbia, Vancouver Is., Sooke River, 7 km N Sooke, N48°27' W123°44', 100 m, May 2009, *T. Goward* 09-232 (UBC). – USA, Oregon, Polk Co, Valley of the Giants, N44°56' W123°43', 365 m, *B. McCune* 30018 (OSC); ibid., Douglas County, BLM Fawn Creek Recreation Area, N43°47' W123°50', 26 m, *B. McCune* 26977 (OSC); ibid., Curry County, Humbug Mountain trail, N42°41' W124°26', 300 m, Sept. 2010, on shaded mossy log in oldgrowth maritime forest, *J. Hollinger* 1385 (UBC).

Notes — No validly published epithet was available to accommodate this species. In northwestern North America, *P. clathrata* shares the neopolydactyla morphotype with several other species including *P. appalachiensis*, *P. nigriventris*, *P. pacifica* and *P. vitikainenii*. The ITS barcode is therefore needed for a reliable identification. Its *Nostoc* cyanobiont is a unique phylogroup (XIb) not known from other *Peltigera* species (Magain et al. 2017a).

***Peltigera holtanhartwigii*** Magain, Miadl. & Sérus., *sp. nov*. — MycoBank MB 845089 ; Fig. 44b–d

*Synonym*. *Peltigera scabrosa* 3a and b in Magain et al. (2017b).

*Etymology*. This new species is dedicated to Jon Holtan-Hartwig for his pioneering work on TLC of *Peltigera*, as well as taxonomic revisions of *Peltigera*, especially in Europe.

*Typus*. RUSSIA, Krasnoyarsk Territory, Reserve 'Stolby', near Fortress rocks, N55°53' E92°46', alt. 1774 ft (acc. 42 ft), June 2012, wet boreal forest with *Abies sibirica*, *Picea obovata*, *Pinus siberica*, grasses, and *Rubus nigra*, on mossy boulder and mossy slope (exposure SW0 along the trail), *J. Miadlikowska et al.* 24.06.2012-L10.3 (holo LE; iso DUKE).

Reference sequence: KX897322.

**Fig. 44** a. *Peltigera clathrata* from Oregon, USA (*B. McCune* 26977, OSC). — b–d. *Peltigera holtanhartwigii*. b. From Greenland (*E. Sérusiaux* DNA 1236, LG); c, d. holotype from Krasnoyarsk, Russia (*J. Miadlikowska et al.* 24.06.2012-L10.3, LE), c. upper and d. lower surface.

*Thallus* conspicuous and large (up to 10 cm diam), or sometimes much smaller, with large rounded lobes up to 1–1.5 cm broad, robust but easily broken when dry; with plane lobe margins. *Upper surface* flat or undulating, typically scabrous, especially towards the margins, greyish to brown when dry, vivid or emerald green when wet (some thalli turn greyish brown or bluish grey color when wet) or not. *Vegetative propagules* not seen. *Lower surface* pale or blackish near lobe margins, with a vein pattern made of poorly delimited veins and interstices. *Rhizines* sparse to abundant, fasciculate or brush-like and usually black. *Apothecia* and *pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: VIIa, VIIc, X (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (absent or trace), dolichorrhizin (absent), zeorin (minor) and accessory 2, 4, 6 and 19 (Fig. 17, S10).

Barcodes — ITS1 (AGACA)**ATATATTC**(CCCC) (Fig. 9).

Ecology — On ground in open tundra or mossy slopes in coniferous forests.

Distribution — Arctic-boreal regions, known from Greenland and Russia (Sakha Republic, Krasnoyarsk territory).

*Specimens examined*. Greenland, Narsarsuaq area, tracks behind the Youth hostel, N61°10' W45°25', 60 m, July 2005, bogs and bushes of *Salix glauca*, *E. Sérusiaux* DNA1236 (LG). – Russia, Krasnoyarsk Territory, Reserve ‘Stolby’, N55° E92°46', 551 m, wet boreal forest with *Abies sibirica*, *Picea obovata*, *Pinus siberica*, *Betula pubescens*, *Rubus nigra*, grasses, *Caltha palustris*, *Carex* spp., and *Equisetum* sp., along mossy boulders and mossy slope along the trail, exposure SW, slope flat, on mossy base of *Betula* (muscicolous), *J. Miadlikowska et al.* DNA-P1536 (DUKE); ibid., Sakha Republic, Verkhoyansk District (Ulus), N67°25' E134°62', 600–700 m, slope of Mt. Mat’-Gora, *Larix cajanderi*-*Pinus pumila* timberline woodland, *T. Ahti* 65068 (H).

Notes — Species delimitation methods recognised two species, *P. scabrosa* 3a and 3b (Magain et al. 2017b) in this lineage; however, our sampling is too poor to circumscribe each separately. Amongst boreal species with a scabrous upper surface, *P. holtanhartwigii* is identified by the presence of dolichorrhizin, peltidatylin and zeorin. The ITS barcode is strongly recommended for a reliable identification.

Similar to *P. borealis* and *P. rangiferina*, two other species with the scabrosa morphotype, *P. holtanhartwigii* can associate with *Nostoc* from phylogroup VIIa, giving the upper surface an emerald green hue when wet. The phylogroup VIIc is shared with other species from the polydactyloid clade (*P. nana* 1) and the dolichorhizoid clade (populations of *P. appalachiensis* in SE USA; see under the description of this species) and phylogroup X is shared with other species from section *Polydactylon* (Magain et al. 2017a). The latter phylogroups give a greyish brown or bluish grey color of the thallus when wet.

*Peltigera holtanhartwigii* is a rare species, currently known from three localities (Greenland, Siberia and East Russia).

### ***Peltigera neopolydactyla*** (Gyeln.) Gyeln., Rev. Bryol. Lichénol. 5: 68. 1932 — MycoBank MB 368953; Fig. 5b, c, 45a, b

*Basionym*. *Peltigera polydactylon* var. *neopolydactylis* (sic !) Gyeln., Magyar Bot. Lapok 31: 46. 1932.

*Synonym*. *Peltigera neopolydactyla* 4 in Magain et al. (2017a, b).

*Typus*. Sweden. ‘Medelpad, Tuna, Allstkullarna, 1928, Ericksson’ (holo ?BPI (no information available); iso S (digital image)) (fide Vitikainen 1994a: 67).

Reference sequence: KX897257.
https://plants.jstor.org/stable/10.5555/al.ap.specimen.s-l1002.

*Thallus* large (8–15 cm across), forming patches consisting of multiple thalli, mostly robust and fragile; lobe margins flat or raised. *Upper surface* slightly undulating, usually wrinkled, sometimes with shallow and irregular concave cavities, smooth, matt; grey or bluish grey to grey brown when dry, more vivid brown to bluish grey when wet. *Vegetative propagules* not seen. *Lower surface* whitish to pale orange or brownish near lobe margins, becoming darker towards the thallus center; veins forming usually a network delimiting regular or irregular interstices, mostly of different shapes and sizes, a pale brownish araneous top layer rarely present near lobe margins, veins raised, usually well delimited pale orange or brown, soon becoming black towards the thallus center. *Rhizines* abundant, long (8–15 mm long), simple or occasionally fasciculate. *Apothecia* frequent, finger-shaped, up to 3–5 mm long, disc reddish brown, with a denticulate margin. *Ascospores* filiform and flexuose, almost cylindrical and becoming thinner towards the ends, 7–9-septate, 81–112 × 3–4 µm (n = 30). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: IV and XIa (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: no peltidactylin, nor dolichorrhizin, zeorin (major) and accessory 2, 6 and perhaps 19 (Fig. 17, S10).

Barcodes — ITS1 (ATTC)**CCCCCG**(CCCT) (Fig. 9).

Ecology — On rocks, logs, mosses or soil in boreal oldgrowth forests.

Distribution — Panboreal to sub-boreal (Norway, Finland, USA/Maine, Japan/Hokkaido, Canada/Québec, Nova Scotia and British Columbia, Russia/Krasnoyarsk and Khabarovsk).

*Selected specimens examined*. Canada, Québec, Minganie County, Côte-Nord, N51°17' W63°50', 373 m, July 2011, boreal forest with *Picea mariana*, on mossy slope, *Miadlikowska*, *Lutzoni*, *Arnold* E200-C3-1 (DUKE-0329794); ibid., Nova Scotia, Lunenburg County, near New Harbour, *F. Anderson* 1340 (NY 00974615); ibid., British Columbia, Clearwater Valley west of Fight Lake, N51°53' W119°56', 1698 m, Aug. 2015, old-growth forests with *Abies lasiocarpa* and *Picea engelmannii*, terricolous at trailside, *T. Goward et al.* 15-21 (UBC); ibid., Clearwater Valley near Caribou Meadow, N51°52' W119°56', 1667 m, Aug. 2015, in old-growth forests with *Abies lasiocarpa* and *Picea engelmannii*, terricolous at trailside, *T. Goward* 15-47 with *C.R. Björk* (UBC). – USA, Maine, Knox County, Vinalhaven, Huber Preserve, N44°5' W68°49', *W.R. Buck* 54962 (NY 01105128). – Finland, Prov. Uusimaa, Tuusula, *O. Vitikainen* 10197b (BG 288709). – Japan, Hokkaido, Kitami Prov., Shari-gun, Sharicho, Shiretoko National Park, N44°6' E145°7', 833 m, *G. Thor* 24306 (UPS L-519471); ibid., Kamikawa, Sounkyo, Daisetsuzan National Park, near Kurodake Trail Head after cable car station, N43°42' E142°54', 1737 m, Aug. 2019, *N. Magain* 8092 (LG). – Norway, Dragasoya, N62°58' E10°54', 300 m, 2011, conifer forest near river, *N. Magain* s.n. (LG); ibid., Buskerud, Sigdal, along the road, near the lake, N60°10' E9°25', July 2011, *N. Magain* P597 (LG); ibid., Oppland, Lillehammer, N61°7' E10°36', 540–600 m, Oct. 1997, on rocky wall in spruce forest, *R. Haugan* 6102 (O-L51997). – Russia, Khabarovsk Territory, Bol’shekhetzkhirskii Reserve, Sosnenskii sector, c. 48 km southwest of Khabarovsk, N48°13' E134°47', 961 m, *J. Miadlikowska* & *F. Lutzoni* 06.2012-P1537 (DUKE).

Notes — The epithet *neopolydactyla* was introduced by Gyelnik (1933) and has been widely applied, especially in the northern hemisphere, to specimens with the neopolydactyla morphotype. Holtan-Hartwig (1993) and Vitikainen (1994a) have already highlighted morphological and chemical heterogeneity of the collections identified as *P. neopolydactyla*. Our study demonstrated that the neopolydactyla morphotype is widespread in section *Polydactylon*, being recorded in eleven often unrelated species in the dolichorhizoid and scabrosoid clades (Fig. 1; Table 3).

The type collection from Sweden was found by Vitikainen (1994a) to represent his chemotype IV (with zeorin only as the main triterpenoid) and morphotype B or C. A single lineage in the scabrosoid clade, *P. neopolydactyla* 4 (Magain et al. 2017a, b) matches these characteristics and contains specimens collected in Scandinavia – obviating the need for epitypification.

Presence of zeorin as the only main triterpene detectable by TLC distinguishes *P. neopolydactyla* from morphologically similar species. Otherwise, it resembles widespread and sympatric

**Fig. 45** a, b. *Peltigera neopolydactyla* from Norway (a. *J. Holtan-Hartwig* 536, O; b. *N. Magain* P597, LG). — c, d. *Peltigera scabrosa*. c. From Norway (*N. Magain* P378, LG); d. from British Columbia, Canada (*C. Bjork* 16230, UBC).

*P. vitikainenii*, with the only difference of having usually thicker, more foveolate thalli with darker veins. The ITS barcode can be very helpful in distinguishing these two species.

Its *Nostoc* phylogroup IV is unique in section *Polydactylon* but common in section *Peltidea*; whereas the phylogroup XIa is shared with closely related *P. scabrosa* and phylogenetically more distant species: *P. scabrosella*, *P. flabellae* and *P. hokkaidoensis* (Magain et al. 2017a).

*Peltigera neopolydactyla* is known throughout the boreal (and oroboreal, sensu Tuhkanen 1984) zone of the northern hemisphere. Collections confirmed with the ITS barcode include Norway, Finland, USA / Maine, Japan / Hokkaido, Canada / British Columbia, Québec and Nova Scotia, Russia / Krasnoyarsk and Khabarovsk. In Europe, *P. neopolydactyla* seems to be absent south of the boreal biome; the existing records from the Alps (Nimis et al. 2018) likely refer to the more widespread and phylogenetically distinct *P. vitikainenii* (see morphological comparison under that species).

**Peltigera rangiferina** Magain, Miadl. & Sérus., *sp. nov.* — MycoBank MB 845090; Fig. 7b, 46a–d

*Synonym*. *Peltigera scabrosa* 4 in Magain et al. (2017a, b).

*Etymology*. This name refers to reindeer (*Rangifer tarandus*), the emblematic animal of the boreal and arctic regions where this new species occurs.

*Typus*. USA, Alaska, Lake Clark National Park, Bay on SW shore of Portage Lake, N60°30' W153°53', 450 m, July 2014, cliffs and broken *Picea* forest near shore, *R. Rosentreter* 18621 (holo OSC; iso DUKE).

Reference sequence: MT659359.

*Thallus* usually conspicuous and large, up to 10–20 cm diam, usually forming regular rosettes, with large rounded lobes (up to 1–2 cm broad), robust but easily broken when dry; with plane or slightly raised margins. *Upper surface* undulating with inconspicuous depressions, typically scabrous, especially towards the lobe margins; grayish to brown when dry, vivid or emerald green when wet. *Vegetative propagules* not seen. *Lower surface* pale, almost white near lobe margins, veins raised or flat, pale brown or orange in marginal zone becoming much darker towards the thallus center, with barely visible interstices. *Rhizines* sparse to usually locally abundant, fasciculate or brush-like, sometimes forming large mats, covering extensive parts of the lower surface. *Apothecia* rare and usually few, finger-shaped, margin hardly denticulate, 4–6 mm long, disc dark reddish brown to almost black. *Ascospores* filiform and flexuose, almost cylindrical and getting thinner towards the ends, 7–9-septate, 83–92(–104) × 3–4 µm (n = 23). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroup VIIa (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (major to trace), dolichorrhizin (trace), zeorin (trace) and accessory 2, 4, 5, 6 and 7 (Fig. 17, S10).

Barcodes — ITS1 (CCCA)**TTACC**(CTCC) (Fig. 9).

Ecology — On mosses or on the ground in boreal forests, arctic and subalpine habitats.

Distribution — Canada (Québec), USA (Alaska), Norway.

*Selected specimens examined*. Canada, Québec, Nunavik, Nord-du-Quebec, N57°55' W72°59', 165 m, July 2011, flat area, open northern limit of boreal forest (5 % forested area), patches with *Picea mariana* (less than 5 m tall), on mosses on ground, *J. Miadlikowska et al.* SN9-C1-2 (DUKE-6159620); ibid., Québec, Baie-James, Nord-du-Quebec, N53°52' E73°, July 2011, 25 % boreal forest / 75 % non-forest vegetation, very widely spaced trees, slightly changed to nearly uniform with understory of Cladonia, canopy cover 20 %, *J. Miadlikowska et al.* SN6-E1 (DUKE). – Norway, Kongsvoll, Mt Knutshø, N62°18' E9°38', 2011, semi-open area with shrubs and a few trees, near a creek, *N. Magain* P549 (LG); ibid., Uldalen, N61°49' E9°37', 800 m, conifer forest near river, 2011, *N. Magain* P529 (LG).

Notes — No validly published epithet was available to accommodate this species. Amongst boreal species with a scabrous upper surface, *P. rangiferina* is also similar to *P. scabrosa* and *P. holtanhartwigii* by the presence dolichorrhizin, peltidatylin and zeorin, and to *P. borealis* by the emerald green color of upper surface of the thallus when wet (due to the presence of *Nostoc* phylogroup VIIa; Magain et al. 2017a). It can often be distinguished by the thallus lower surface which is very pale and essentially veinless near the lobe tips, becoming black and without visible interstices towards the thallus center. The ITS barcode is recommended for a reliable identification.

*Peltigera rangiferina* is widespread but rare in boreal forests and adjacent habitats, as well as in arctic and subalpine habitats in the northern hemisphere above 60° latitude North in Scandinavia, Canada and Alaska. So far, it has not been found in Asia.

**Peltigera scabrosa** Th. Fr., Lichenes Arctoi (Groenlandiaeque hactenus cogniti): 45. 1860 — MycoBank MB 399356; Fig. 45c, d

*Synonym*. *Peltigera scabrosa* 2 in Magain et al. (2017a, b).

*Typus*. Greenland, Breutel, Flora Germaniae Exsiccati 203, UPS (lectotype selected by Vitikainen 1994a: 80; n.v.).

Reference sequence: OM913602.

*Thallus* usually conspicuous and large, up to 10–20 cm diam, usually forming regular rosettes, with large rounded lobes up to 1–2 cm broad, robust but easily broken when dry; with plane or slightly raised lobe margins. *Upper surface* undulating with inconspicuous depressions, typically scabrous, especially towards the lobe tips; greyish to brown when dry, with more intense colors when wet, but never emerald green. *Vegetative propagules* not seen. *Lower surface* pale, almost white near the lobe margins, with a distinct vein pattern highly contrastive with the paler interstices, veins raised, sometimes strongly, pale brown or orange near lobe margins becoming much darker towards the thallus center. *Rhizines* sparse to locally abundant, fasciculate or rarely simple. *Apothecia* sometimes present, abundant, finger-shaped, margin hardly denticulate, 4–6 mm long, disc dark reddish. *Ascospores* filiform and flexuose, almost cylindrical and becoming thinner towards the ends, 7-septate, 98–119 × 3–4 µm (n = 22). *Pycnidia* not seen.

Photobiont — *Nostoc* phylogroups: XIa and VIId (Magain et al. 2017a).

Chemistry — Tenuiorin (major), methylgyrophorate (major) and gyrophoric acid (trace); triterpenes: peltidactylin (major), dolichorrhizin (minor), zeorin (trace or absent) and accessory 2, 5 and 6 (Fig. 17, S10).

Barcodes — ITS1 (CTGC)**AAACCCCCAAC**(CCTT) (Fig. 9).

Ecology — Mainly overgrowing mosses on soil in boreal forests or heathlands, rarely on mossy rock outcrops.

Distribution — Norway, Finland, Iceland, Greenland; USA (Alaska), Canada (Alberta, British Columbia and Québec); Russia (Krasnoyarsk Territory and Komi Republic).

*Selected specimens examined*. Canada, Québec, N56°32' W73°13', July 2011, *F. Lutzoni et al.* 2011-P107 (DUKE); ibid., N56°32' W73°20', July 2011, *F. Lutzoni et al.* 2011-P113 (DUKE); ibid., British Columbia, Coast Ranges, Southgate Valley, N50°53' W124°48', 10 m, June 2007, cliff near estuary, *C.R. Björk* 14564 (UBC); ibid., Sunshine Coast, E shore of Agamenon Channel on mainland, N49°42' W124°4', 10 m, July 2008, moderately shaded rock outcrop above high tide line, *C.R. Björk* 17053 (UBC); ibid., Peace River Valley, c. 19 km west of town of Fort St. John, 615324 6234089 Z10, 500 m, July 2008, cut bank on river shore, *C.R. Björk* 16230 (UBC). – Greenland, Narsarsuaq area, tracks behind the Youth hostel, N61°10' W45°25', 60 m, July 2005, bogs and bushes of *Salix glauca*, *E. Sérusiaux* s.n. (LG). – USA, Alaska, Lake and Peninsula Co, Katmai National Park, near Brooks Camp, N58°33' W155°47', 18 m, *Picea glauca* forest and edge of fen, July 2013, *K. Spickerman* 133 (OSC). – Iceland, Hveradalur Kerlingarfjollum, N64°38' W19°16', 90–95 m, *H. Kristinsson* (LA-30062). – Norway, Buskerud, Sigdal,

**Fig. 46** *Peltigera rangiferina*. a, b. From Norway (*N. Magain* P529, LG), a. upper and b. lower surface; c, d. holotype from Alaska, USA (*R. Rosentreter* 18621, OSC).

along the road, near the lake, N60°10' E9°25', July 2011, *N. Magain* P378 (LG). – Finland, Muonio, Muonio, along Pallaksentie road, on the edge of Pallas-Yllästunturi National Park, near the parking lot, N67°57' E24°3', Aug. 2016, on soil, in boreal forest (taiga), *A. Simon* 73 (LG). – Russia, Komi Republic, Troitsko-Pechorskii, N62°38' E58°45', 600–720 m, June 2003, terricolous on small slate rocks at low subalpine zone, *J. Hermansson* 12628 (UPS 264900); ibid., Gorod Inta, Yugyd Va National Park, Missuviza river, N65°51' E60°37', Sept. 2019, *Salix* stand in swampy deciduous forest, epigeic on ground by roadside, *I. Jüriado* 475 (TUF088254); ibid., Krasnoyarsk Territory, Reserve 'Stolby', on trail going to Bariery Rocks, N55°54' E92°46', 1853 ft, June 2012, mesic forest with *Abies sibirica* and *Betula pubescens*, on mosses on rocky cliff of a monolith facing S, *F. Lutzoni* & *J. Miadlikowska* 06.24.2012-P1540 (DUKE).

Notes — Magain et al. (2017a, b) demonstrated that a scabrous upper surface was present in multiple unrelated lineages representing well-supported species in section *Polydactylon*, i.e., *P. pulverulenta*, *P. truculenta* var. *autroscabrosa* and *P. scabrosella* within the dolichorhizoid clade, and *P. borealis*, *P. holtanhartwigii*, *P. rangiferina* and *P. scabrosa* intermixed with the non scabrous *P. clathrata* and *P. neopolydactyla* s.str. in the scabrosoid clade.

The lectotype of *P. scabrosa* was chosen by Vitikainen (1994a) and refers to the most common chemotype I of Holtan-Hartwig (1993), which is characterised by the presence of dolichorrhizin, peltidactylin and zeorin. An ITS sequence from the lectotype confirmed that it is conspecific to *Peltigera scabrosa* 2 (Magain et al. 2017a, b), the most common species in Northern Europe, which displays chemotype I.

Amongst boreal species with a scabrous upper surface, *P. scabrosa* is characterised by the presence of dolichorrhizin, peltidactylin and zeorin, its dull (never emerald green) upper surface when wet, and its highly contrastive interstices on the lower surface; in the other three species (*P. borealis*, *P. holtanhartwigii* and *P. rangiferina*), the veins are less distinct and sometimes hidden under a mat of rhizines.

*Peltigera scabrosa* shares *Nostoc* phylogroup XIa with *P. scabrosella* and *P. neopolydactyla* s.str., but phylogroup VIId was not detected elsewhere in section *Polydactylon* (Magain et al. 2017a).

*Peltigera scabrosa* is widespread in forests and more open habitats in boreal and arctic localities. It is known from northern Europe, northern North America (mainly Canada; rare in USA) and East Russia. In Québec, where it co-occurs with the more widespread *P. borealis* (between 48 and 55 °N), it is restricted to most northern localities (> 56 °N) (Lu et al. 2018). It has been reported from the Alps in Europe (Nimis et al. 2018), but the only collection we examined represents *P. borealis* (see under that species).

## ADDENDUM

**_Peltigera polydactylon_** (Neck.) Hoffm., Descr. Adumb. Plant. Lich. 1(1): 19. 1789 '1790' — MycoBank MB 399347

*Basionym. Lichen polydactylon* Neck. (as '*polydactilon*'), Method. Muscor.: 85. 1771.

**_Peltigera polydactylon_** subsp. **_udeghe_** Magain, Miadl. & Sérus., Herzogia 29(2/1): 518. 2016 — MycoBank MB 817321

*Typus.* Russia, Khabarovsk Territory, Durminskoye forest-hunting area, c. 200 km SSE of Khabarovsk, North of Durmin Mt., Rovnyi Creek valley, adjacent to foothills of the Sikhote-Alin' Range Mountains, N47°49' E135°58', 328 m, July 2013, stand of *Picea ajanensis* forest with *Pinus koraiensis* and *Abies nephrolepis* in otherwise broadleaf forest with extensive ground cover by ferns and mosses, over mosses and plant debris on ground, *J. Miadlikowska* & *F. Lutzoni* 07.30.2013-P3033 (holo DUKE (DNA-P3033)).

Reference sequence: KX365430.

*Synonym. Peltigera polydactyla* var. *conjungens* Müll.Arg., Flora 66: 22. 1883 — MycoBank MB 532350.

*Typus.* Australia, Queensland, Toowoomba, *C.H. Hartmann* s.n. (G! specimen G00053915, lectotype designated by Louwhoff 2008, following an annotation by Vitikainen in 1973).

Reference sequence: OM913601.
https://plants.jstor.org/stable/10.5555/al.ap.specimen.g00053915.

Notes — The ITS sequence of the lectotype of *Peltigera polydactyla* var. *conjungens* clearly matches *P. polydactylon*

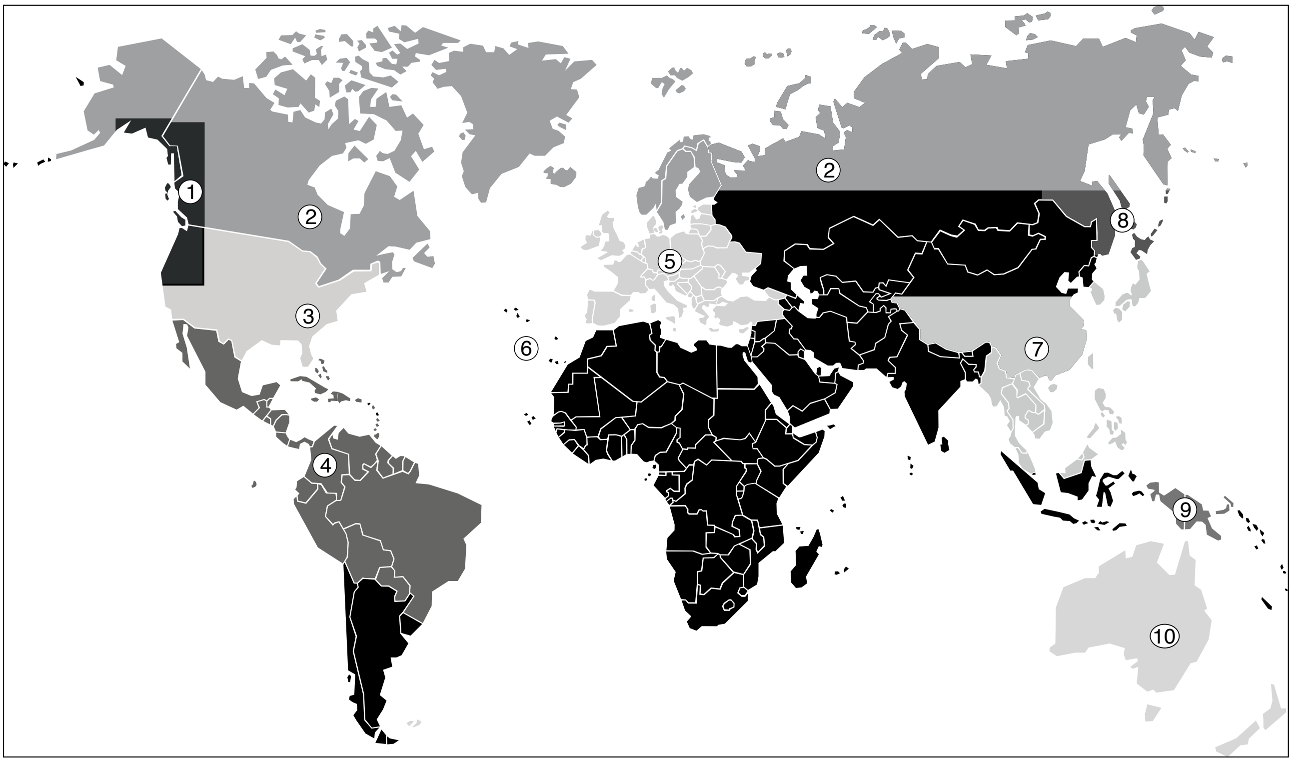

**Fig. 47** Schematic geographical map showing the regions covered by the identification keys. Numbers follow the sections of the key. Regions in black are not covered. The map is intended as a visual guide and regions are schematic, with no purpose of precise geographic delimitation between regions.

subsp. *udeghe*. At the rank of subspecies, the epithet *udeghe* has priority over *conjungens.*

## KEY TO THE SPECIES OF PELTIGERA SECTION POLYDACTYLON

The following species with a glabrous upper surface of the thallus do not belong to section *Polydactylon* but can be confused morphologically: *Peltigera degenii* and non-tomentose morphs of *P. praetextata* from section *Peltigera*, but both species have raised veins typical of section *Peltigera*, and no secondary metabolites detectable in TLC; *P. horizontalis* and *P. elisabethae* from section *Horizontales*, but both species have fasciculate rhizines distributed in concentric rows and horizontally oriented ellipsoid apothecia (wider than long); *P. neckeri* and *P. collina* from section *Horizontales*, but both species have diffuse and soon becoming black venation and black apothecia; *P. malacea* from section *Peltidea*, but it has an erect tomentum on the marginal upper surface of the thallus, which can also become scabrous like in *P. scabrosa*, however, the latter species is never tomentose.

Because of strong geographic patterns detected in section *Polydactylon*, the keys are organized by geographic regions (Fig. 47). For several regions, only one species of this section is known: *P. dolichorhiza* for Africa, including Madagascar and the Mascarene archipelago, but excluding Macaronesia; *P. truculenta* (var. *austroscabrosa* if thallus scabrous) for Argentina and Chile south of the S 33° latitude; *P. hawaiiensis* for the Hawaii archipelago.

Intraspecific plasticity is important in section *Polydactylon*, and several species may be undistinguishable morphologically. The following keys should be used with caution and we recommend sequencing ITS or performing TLC to confirm species identifications in most cases.

The Tree-Based Alignment Selector (T-BAS v. 2.1, https://tbas.hpc.ncsu.edu/; Carbone et al. 2019) includes a multilocus global *Peltigera* reference tree based on seven loci (ITS, β-tubulin, *RPB1*, LSU, COR1b, COR3 and COR16; Chagnon et al. 2019). Unidentified *Peltigera* individuals for which at least one of these loci is available can be identified using the evolutionary placement algorithm (EPA) performed on this tree directly on the portal.

### 1. Key to the species of humid northwestern North America

(south-east Alaska, British Columbia, Oregon, Washington, Northern California, Idaho, Montana)

1. Phyllidia present (along lobe margins or at the margins of the stress cracks)[1] . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
1. Phyllidia absent . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
2. Polydactylon morphotype: thallus rather thick with dark brown veins extending to the lobe margins . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. polydactylon* subsp. *udeghe*
2. Neopolydactyla morphotype: thallus rather thin with light brown/orange veins usually not extending to the lobe margins . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. pacifica*
2. Hymenina morphotype: lower surface with pale margins and hardly visible veins and interstices . . . . . . . . *P. hymenina*
3. Upper surface scabrous[2] . . . . . . . . . . . . . . . . . . . . . . . . . 4
3. Upper surface not scabrous. . . . . . . . . . . . . . . . . . . . . . . 5
4. Upper surface dark grey to dark brown, sometimes olivaceous but never emerald green when wet; veins usually distinct with well-delimited interstices . . . . . . *P. scabrosa*
4. Thallus thinner with usually smaller lobes up to 15 mm wide; veins dark brown, distinct, with well delimited small white interstices disappearing towards the margins and becoming black and fused towards the center; rhizines short and black; rare species only known from Alaska . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. rangiferina*
5. Hymenina morphotype: lower surface with pale margins and hardly visible veins and interstices . . . *P. hymenina*
5. Neopolydactyla or occidentalis morphotypes: veins and interstices well visible . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6
6. Thallus thick; lower surface with a distinct network of very dark veins reaching or almost reaching the margins . . 7
6. Thallus thinner; lower surface with light brown or dark brown veins not reaching the margins or becoming paler towards the margins . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8
7. Upper surface scrobiculate, with large and irregular depressions; lower surface with a dense network of rather broad, strongly raised dark brown to black veins delimiting large interstices . . . . . . . . . . . . . . . . . . . . . . . . . . *P. clathrata*
7. Lower surface with distinct elliptical interstices (3–4 × c. 2 mm long when well-developed) in between a dense network of rather broad, diffuse, flat or slightly raised, dark brown to black veins . . . . . . . . . . . . . . . . . *P. nigriventris*
8. Thallus fan-shape, greenish brown when dry; the arrangement of the apothecia along the lobes resembles open hand fingers; lower surface pale throughout; only known from British Columbia (Canada) . . . . . . . . . . *P. flabellae*
8. Thallus different from above . . . . . . . . . . . . . . . . . . . . 9
9. Upper surface emerald green, or at least with a distinct shade of green when moist . . . . . . . . . . . . . . . . . . . . . 10
9. Upper surface bluish greyish (not green) when moist . 11
10. Occidentalis morphotype: lower surface with veins soon becoming black towards the center delimiting a network of oval or diffuse interstices . . . . . . . . . . . *P. occidentalis*
10. Neopolydactyla morphotype: lower surface without such a network . . . . . . . . . . . . . . . . . . . . . . . . *P. appalachiensis*
11. Lower surface with white margins and light brown to orange veins becoming white towards the margins; phyllidia sometimes present along the lobe margins. . . *P. pacifica*
11. Lower surface with light brown to dark brown veins, not becoming white towards the margins, phyllidia not present[3] . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. vitikainenii*

### 2. Key to boreal species

1. Upper surface scabrous . . . . . . . . . . . . . . . . . . . . . . . . . 2
1. Upper surface not scabrous . . . . . . . . . . . . . . . . . . . . . 5
2. Thallus usually small with lobes usually 10–15 mm wide; lower surface pale throughout the entire or almost the entire thallus, veins pale, rhizines arranged in flaky mats; in wet ecological conditions; at low elevations. . . *P. scabrosella*
2. Thallus usually large with lobes often up to 20 mm wide (if smaller, compare *P. rangiferina*); lower surface dark towards the thallus center, either with distinct or fused veins; in variable ecological conditions . . . . . . . . . . . . . . . . . 3
3. Upper surface dark grey to dark brown, sometimes olivaceous but never emerald green when wet; veins usually distinct with well-delimited interstices; chemotype with peltidactylin, dolichorrhizin and usually zeorin; common in Northern Europe and Western North America but rare

---

[1] Phyllidiate species from section *Peltigera* (e.g., *P. praetextata*, *P. wulingensis*) also occur in this region, but their thalli are usually tomentose at least at the lobe margins and the lower surface of the thallus is different (raised veins and rhizines differently shaped).

[2] Other scabrous species: *P. borealis* and *P. holtanhartwigii* (the latter found in more northern localities in Alaska) have not been reported from this region, however, they may occur there.

[3] *Peltigera neopolydactyla* s.str. has not been reported from northwest North America.

in the northern latitudes in Eastern North America . . . . . . . . . . *P. scabrosa*

3. Thallus with greenish to emerald green upper surface when wet (scabrosity sometimes makes the color rather dim) 4

4. Thallus usually rather thick with large lobes up to 20 mm wide; veins not well visible with large and poorly delimited interstices; lower surface usually covered by a thick mat of dark rhizines; zeorin present, peltidactylin and dolichorrhizin absent; common in North America, rare in Europe . . . . . . . . . . *P. borealis*
4. Thallus thinner with usually smaller lobes up to 15 mm wide; veins dark brown, distinct, with well delimited small white interstices disappearing towards the margins and becoming black and fused towards the center; rhizines short and black; peltidactylin, dolichorrhizin and zeorin present; rare species . . . . . . . . . . *P. rangiferina*
4. Lower surface mostly dark brown to black because of the fused vein pattern delimiting short white ellipsoid interstices; rhizines fasciculate to brush-like; peltidactylin, dolichorrhizin and zeorin present; rare species found only in very northern latitudes . . . . . . . . . . *P. holtanhartwigii*

5. Polydactylon morphotype: lower surface with a network of dark brown veins extending to lobe margins . . . . . . . . . 6
5. Neopolydactyla or hymenina morphotypes: lower surface different from the above . . . . . . . . . . 8

6. Thallus usually with marginal phyllidia (often abundant); present in North America and Eastern Russia . . . . . . . . . . *P. polydactylon* subsp. *udeghe*
6. Thallus without phyllidia . . . . . . . . . . 7

7. TLC with an unidentified terpenoid showing a pink spot between peltidactylin and tenuiorin in phase C, known from Norway and Finland but expected elsewhere, rare species . . . . . . . . . . *P. seneca*
7. TLC without such a pink spot, known from Europe and Eastern Asia, common species . . . . . . . . . . *P. polydactylon* subsp. *polydactylon*

8. Hymenina morphotype: lower surface with pale margins and hardly visible veins and interstices; in oceanic regions of Europe and Eastern and Western North America . . . . . . . . . . *P. hymenina*
8. Neopolydactyla morphotype . . . . . . . . . . 9

9. Upper surface emerald green when wet . . . . . . . . . . 10
9. Upper surface dark brown, black, grey or bluish when wet . . . . . . . . . . 11

10. Lower surface with veins soon becoming black towards the thallus center delimiting a network of oval or diffuse interstices (occidentalis morphotype) . . . *P. occidentalis*
10. Veins not fused except the central part of the thallus, forming an irregular network of regular or irregular large interstices usually of various shape and size; common in North America, rare in Europe and Asia . . . . *P. appalachiensis*

11. Thallus usually rather thick with upper surface wrinkled, black to dark brown; zeorin present, dolichorrhizin and peltidactylin absent; common in Europe, present in East Asia and Eastern North America . . . . . *P. neopolydactyla*
11. Thallus usually rather thin with upper surface grey to bluish when wet; dolichorrhizin, peltidactylin and zeorin almost always present; common in Europe and Asia, rare in North America (known only from the Pacific West Coast) . . . . . . . . . . *P. vitikainenii*

### 3. Key for the Appalachian Mountains (North America)

1. Thallus small with narrow lobes; veins dark, well visible but becoming paler toward the thallus margins, interstices small and oval; polydactylon morphotype, rare . . . . . . *P. seneca*
1. Thallus usually large with broad lobes . . . . . . . . . . 2

2. Neopolydactyla or polydactylon morphotypes; thallus large; lower surface with a network of brown veins delimiting large interstices; common . . . . . . . . . . *P. appalachiensis*
2. Mostly typical occidentalis morphotype; veins more fused delimiting smaller ellipsoid interstices; rare *P. occidentalis*

### 4. Key for the Neotropics

1. Upper surface smooth or almost smooth . . . . . . . . . . 2
1. Upper surface scabrous (pulverulenta morphotype) . . . . 6

2. Phyllidia present and mostly on raised and crisped lobe margins; dolichorhiza morphotype . . . . . . . . . . *P. kukwae* var. *phyllidiata*
2. Phyllidia absent; dolichorhiza, neopolydactyla, occidentalis or atypical morphotypes . . . . . . . . . . 3

3. Lower surface usually with a network of very dark brown veins delimiting small interstices or veins fused and interstices not visible . . . . . . . . . . 4
3. Lower surface usually with dark brown veins delimiting large interstices . . . . . . . . . . 5

4. Occidentalis morphotype; terricolous; known from central America and the northern parts of the Andes *P. esslingeri*
4. Stanleyensis or atypical morphotypes; terricolous or saxicolous; known from the Andes and Brazil/Minas Gerais . . . . . . . . . . *P. massonii*

5. ITS barcode (AGGTT)**GTACAT**(AGAG) (Fig. 9); dolichorhiza morphotype but populations with robust thalli were also seen (neopolydactyla morphotype); rhizines sometimes long and robust covering almost the entire lower surface but leaving interstices visible . . . . . . . . . . *P. dolichorhiza*
5. ITS barcode (GAAA)**CCTAGT**(TGGATGT) (Fig. 9); dolichorhiza morphotype; exclusively terricolous; known from Central America, the Carribean and the northern parts of the Andes . . . . . . . . . . *P. borinquensis*
5. ITS barcode (AAAGC)**TGTAGGA**(TAAAAAA) (Fig. 9); atypical dolichorhiza morphotype similar to hymenina morphotype; veins not raised and poorly delimited forming a rather dense network towards the margins with hardly visible interstices; rhizines quite long (0.8–1 cm), dark brown to black, fasciculate to brusk-like, becoming fibrillose, abundant and sometimes forming dense mats toward the thallus center; known only from SE Brazil . . . . . . . . . . *P. itatiaiae*
5. ITS barcode (GGG)**ATAAAAAAGACTATGAAA**(CCTATGA) (Fig. 9); dolichorhiza morphotype; variable morphology, known from SE Brazil and the Andes (Ecuador) . . . . . . . . . . *P. kukwae* var. *kukwae*

6. ITS barcode (GGTTGT)**CATAAGAA** (Fig. 9); pulverulenta morphotype; common . . . . . . . . . . *P. pulverulenta*
6. ITS barcode (CGAAA)**TGGGTTC**(TTCTTGG) (Fig. 9); pulverulenta morphotype; rare . . . . . . . . . . *P. willdenowii*
6. ITS barcode (TTGCCC)**AGAAAA**(CTACCT) (Fig. 9); pulverulenta morphotype; rare . . . . . . . . . . *P. sipmanii*

### 5. Key for Temperate Continental Europe (excluding Fennoscandia; see key 2)

1. Thallus scabrous; peltidactylin and dolichorrhizin absent; very rare in high altitudes in the Alps . . . . . . . . . *P. borealis*
1. Thallus not scabrous[1] . . . . . . . . . . 2

2. Polydactylon morphotype: lower surface with dark brown veins extending to the lobe margins, apothecia dark brown . . . . . . . . . . *P. polydactylon* subsp. *polydactylon*
2. Neopolydactyla or hymenina morphotypes, apothecia orange or light brown . . . . . . . . . . 3

---

[1] The presence of *P. neopolydactyla*, *P. occidentalis* and *P. scabrosa* in the European Alps and the Carpathians Mountains was not confirmed.

3. Hymenina morphotype: lower surface with pale margins and hardly visible veins and interstices; common in the oceanic regions; morphotype similar to neopolydactyla occurs in Northern Great Britain . . . . . . . . . . *P. hymenina*
3. Neopolydactyla morphotype; rare in montane areas . . . . . . . . . . *P. vitikainenii*

### 6. Key for Macaronesia

1. Polydactylon morphotype: thallus rather thick, brownish grey; lower surface with dark brown veins extending to the margins, dark brown apothecia . . . . . . . . . . *P. polydactylon* subsp. *polydactylon*
1. Hymenina or neopolydactyla morphotypes, apothecia orange or light brown . . . . . . . . . . 2
2. Morphotype similar to neopolydactyla; lower surface whitish to pale orange with diffuse, hardly visible and flat veins forming a dense irregular network with irregular whitish interstices; rhizines very dark forming a clear contrast with the pale lower surface; restricted to the Azores . . . . . . . . . . *P. melanorrhiza*
2. Hymenina morphotype . . . . . . . . . . 3
3. Hymenina morphotype: thallus bluish grey, sometimes very thin; folioles sometimes present; corticolous, saxicolous or terricolous across all three archipelagos . . . . . . . . . . *P. hymenina* var. *hymenina*
3. Hymenina morphotype; thallus almost white or pale bluish when wet consisting of small lobes with raised margins and abundant marginal phyllidia; apothecia small and usually abundant; exclusively epiphytic in the Azores . . . . . . . . . . *P. hymenina* var. *dissecta*

### 7. Key for tropical and subtropical Southeast Asia (incl. China/Yunnan, Taiwan, Japan/Honshu) (very preliminary until the revision of the polydactyloid clade is completed)

1. Upper thallus with patches of scattered, minute whitish crystals . . . . . . . . . . 2
1. Upper thallus without whitish crystals . . . . . . . . . . 4
2. Tenuiorin and methylgyrophorate absent, dolichorrhizin present; upper surface smooth, margins pruinose or strongly incrusted (Fig. 48d, 49) . . . . . . . . . . *P. dolichospora*
2. Tenuiorin and methylgyrophorate always present . . . . . . 3
3. ITS barcode **GTTGTACAA** (Fig. 9) . . . . . . . . . . *P. asiatica*
3. Other ITS barcode (Fig. 9) . . . . . . . . . *P. nana* and *P.* sp. 8 . . . . . . . . . . (Fig. 48a–c, 50) (unresolved species complexes in the polydactyloid clade)
4. Occidentalis morphotype at the lower surface: the rhizines branched and fasciculate and not forming flocculent masses; otherwise neopolydactyla morphotype; known only from Honshu/Japan . . . . . . . . . . *P. orientalis*
4. Dolichorhiza or polydactylon morphotype: large brittle thallus; veins dark brown to black extending to the lobe margins and forming a strong contrast with the pale undersurface; rhizines simple to slightly fasciculate . . . . . . . . . . 5
5. ITS barcode (CAG)**GTTGTACAA**(GGTTG) (Fig. 9); southern regions (Borneo, Yunnan, Taiwan, Vietnam) . . . *P. asiatica*
5. ITS barcode (ACC)**TCTCTTA**(TGAAG) (Fig. 9); northern regions (Yunnan, Taiwan, Japan and Russia) . . *P. mikado*

### 8. Key for northern parts of East Asia (Japan/Hokkaido, Russia/Khabarovsk and Sakhalin)

1. Occidentalis morphotype: thallus emerald green when wet in northern localities; veins becoming black towards the thallus center and forming a network with oval or diffuse interstices . . . . . . . . . . *P. occidentalis*
1. Thallus dark brown, black, grey or bluish but never emerald green when wet . . . . . . . . . . 2
2. Marginal phyllidia usually present and abundant; veins brownish but usually not pale orange brown . . . . . . . . . . *P. polydactylon* subsp. *udeghe*
2. Marginal phyllidia absent . . . . . . . . . . 3
3. Upper thallus usually with patches of scattered, minute whitish crystals . . . . . . . . . . 4
3. Upper thallus without patches of scattered, minute whitish crystals . . . . . . . . . . 5
4. ITS barcode (ACC)**TCTCTTA** (TGAAG) (Fig. 9) *P. mikado*
4. ITS barcode different *P. nana* and *P.* sp 8 (Fig. 48a–c, 50) . . (unresolved species complex in the polydactyloid clade)
5. Neopolydactyla morphotype: thallus rather robust and thick . . . . . . . . . . *P. neopolydactyla*
5. Thallus fragile and brittle . . . . . . . . . . 6
6. ITS barcode (CACA)**AGAAAGC**(ATCGG) (Fig. 9); lower surface pale (whitish to pale orange brown), usually epiphytic . . . . . . . . . . *P. hokkaidoensis*
6. ITS barcode (TTAT)**CGAGGA**(CATGT) (Fig. 9); lower surface pale near the lobe margins and becoming darker toward the center; dense network of rather large, diffuse, slightly raised, dark brown to black veins and distinct elliptical interstices . . . . . . . . . . *P. chabanenkoae*
6. ITS barcode (CTTGG)**GCATATAAA**(GCTGT) (Fig. 9); lower surface whitish to pale orange near the lobe margins and becoming darker towards the center, veins forming an irregular network . . . . . . . . . . *P. vitikainenii*

### 9. Key for Australia and New Zealand (very preliminary until more material is available)

1. Mostly dolichorhiza or neopolydactyla morphotypes but occasionally polydactylon morphotype; variable morphology; ITS barcode **CCAAAG**(CATT) (Fig. 9); very common . . . . . . . . . . *P. gallowayi*
1. Polydactylon morphotype . . . . . . . . . . 2
2. Marginal phyllidia usually present . . . . . . . . . . *P. polydactylon* subsp. *udeghe*
2. Marginal phyllidia usually absent; upper surface with pruina (patches of scattered, minute whitish crystals); rare, perhaps species complex . . . . . . . . . . *P.* cf. *nana*

### 10. Key for Papua New Guinea
(see Sérusiaux et al. 2009 for further details)

1. Thallus small with marginal soralia; dolichorrhizin and zeorin present; terricolous . . . . . . *P. weberi* (polydactyloid clade)
1. Thallus without marginal soralia . . . . . . . . . . 2
2. Tenuiorin and methylgyrophorate absent but terpenoids present (at least dolichorrhizin); upper surface smooth, sometimes slightly pruinose or incrusted at the lobe margin; lobes with raised and crisped lateral margins . . . . . . . . . . *P. oceanica* (polydactyloid clade)
2. Tenuiorin and methylgyrophorate always present, as well as terpenoids . . . . . . . . . . 3
3. Rhizines rather short, fasciculate or densely branched, usually abundant, rarely sparse . . . . . . . . . . 4
3. Rhizines usually long and simple, sparse or abundant . . 5
4. Stanleyensis morphotype: thallus brittle with a dark brown shiny surface, slightly undulating; lower surface with flat dark veins leaving almost no interstices; dolichorrhizin absent or present in a low quantity . . . . . . . . . . *P. stanleyensis*
4. Atypical stanleyensis morphotype: thallus rarely brittle, upper surface shiny or not, sometimes distinctly pruinose; veins broad and fused, usually jet black with elliptical and whitish

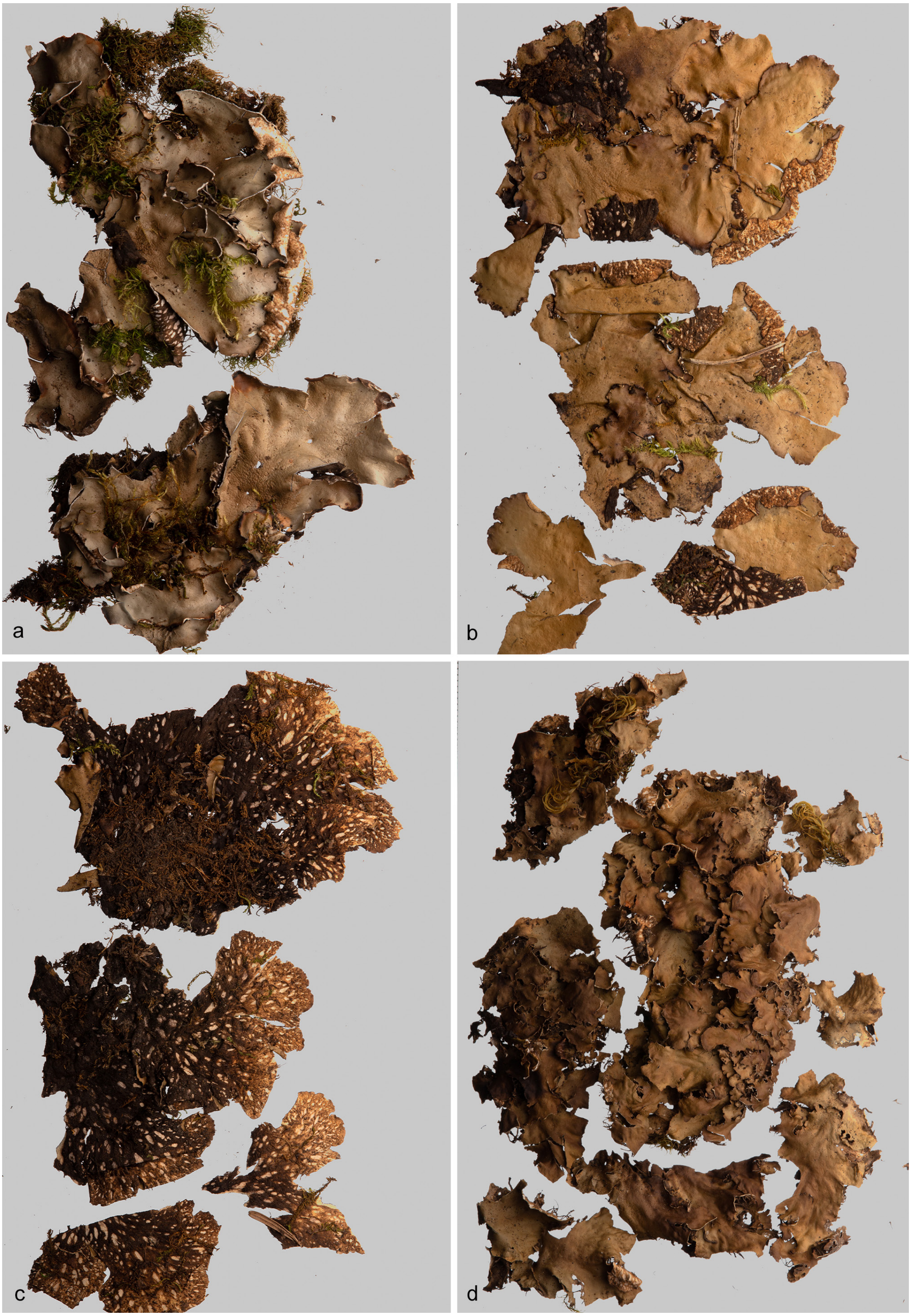

**Fig. 48** a–c. *Peltigera* sp. 8. a. Thallus from South Korea (*G. Thör* 20581, UPS); b. upper and c. lower surface of sample pruinose from South Korea; d. *Peltigera dolichospora* (*J. Miadlikowska* P1297, DUKE) from Yunnan, China.

**Fig. 49** *Peltigera dolichospora*. a. Upper and b. lower surface of *B. Goffinet* 10108 (CONN) from Yunnan, China. c. Upper and d. lower surface of *B. Goffinet* 10101 (CONN) from Yunnan, China.

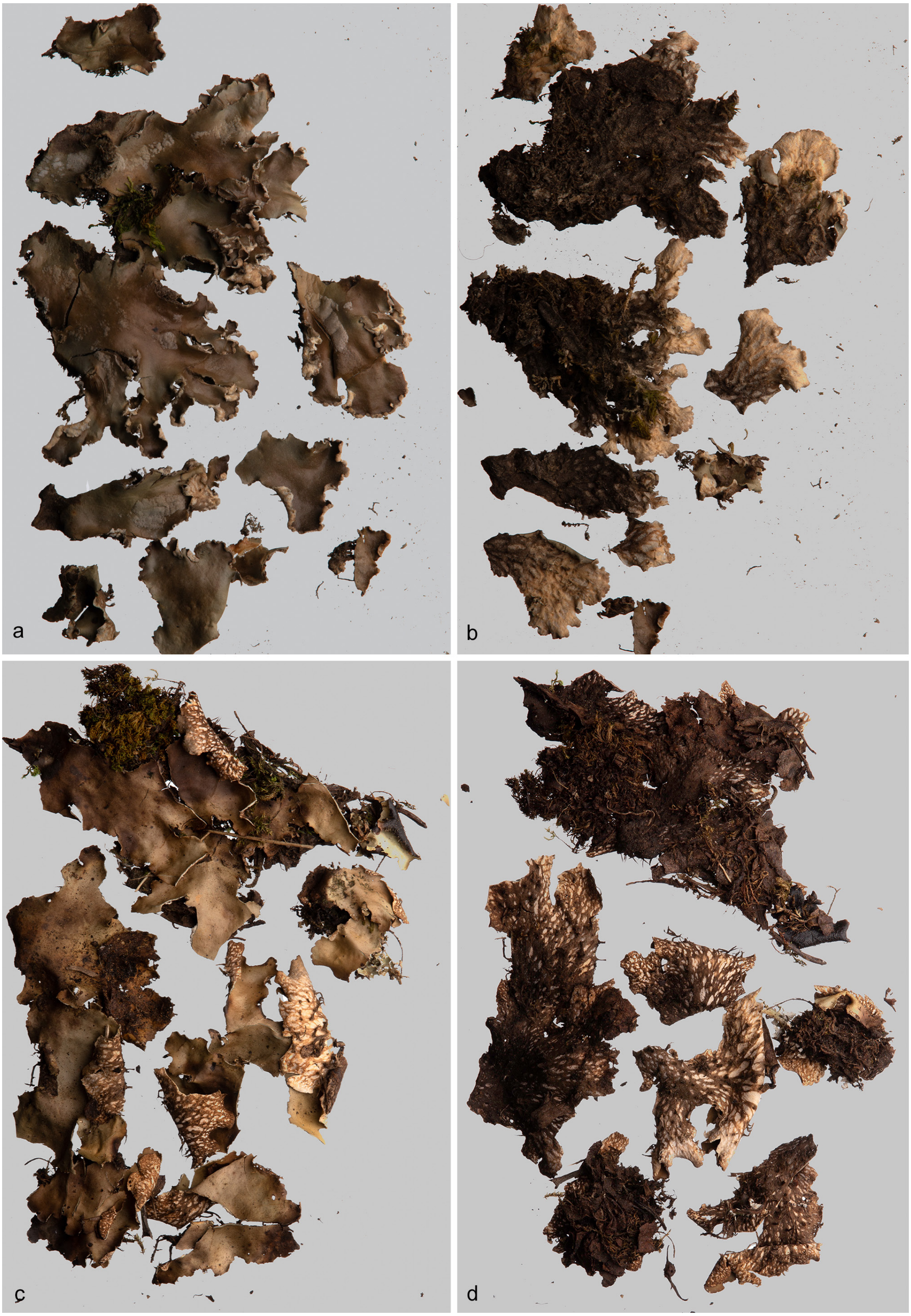

**Fig. 50** a. Upper and b. lower surface of *Peltigera nana* (*G. Thör* 21255, UPS) from South Korea. c. Upper and d. lower surface of of *Peltigera* sp. 8 (*B. Goffinet* 9978, CONN) from Yunnan, China.

interstices; rhizines fasciculate and densely branched; dolichorrhizin in large quantity . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. sumatrana* (polydactyloid clade)

5. Thallus robust, not distinctly undulated; upper surface usually with pruina at the lobe margins and sometimes with large and conspicuous incrusted patches; lower surface with a dense network of flat, dark veins and distinct rather small, elliptical, whitish interstices; dolichorrhizin is the main terpenoid; terricolous . . . . . . . . . . . . . . *P. nana* (polydactyloid clade)
5. Thallus fragile, distinctly undulating surface with shallow depressions; lower surface with a loose network of raised, pale to dark veins with large, elliptical, whitish to pale orange interstices; several chemotypes observed; mostly epiphytic, rarely on rotten wood or on terricolous mosses . . . . . . . 6
6. Dolichorrhizin present in large quantity; thallus usually rather thick, with a *P. polydactylon* morphotype lower surface where the veins extend to the lobe margins and the interstices exceed the width of the veins toward the thallus center but become narrower than the veins towards the lobe tips . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. serusiauxii*
6. Dolichorrhizin absent; dolichorhiza morphotype . . . . . . . 7
7. Zeorin and peltidactylin present . . . . *P. dolichorhiza* s.lat. A (undescribed species belonging to the dolichorhizoid clade)
7. Four unknown terpenoids including unidentified green and red spots visible on TLC plates . . . . . . . . . . . . . . . *P. elixii*

**Acknowledgments** This work was supported by the National Science Foundation (DEB-1025930 REVSYS, DEB-1046065 Dimensions, DEB-1556995 SG, DEB-1541548 GoLife, and DEB-1929994 BEE to FL and JM). We would like to thank all collectors and curators of herbaria who provided material for this study including the following herbaria: AMNH, ANDES, B, BG, BORH, BR, CANB, CBG, CDS, CGMS, CONC, CONN, DUKE, F, G, H, KOBL, LA, LE, LG, MA, MAF, MEXU, MHA, NSPM, NY, O, OMA, OSC, PERTH, PMAE, QFA, SAKH, TAIE, TUF, UBC, UDBC, UGDA, UPS and W.

Special thanks to A. Aptroot, D. Ertz, P. Divakar, E. Gaya, R. Darnajoux, M. Sohrabi, C. Truong, J. Hollinger, F. Bungartz, M. Kukwa, B. McCune for sending us interesting specimens. Thanks to M. Marcelli and M.J. Kitaura for assistance during the field trip in Minas Gerais, Brazil, as well as S. Restrepo, E.A. Soto Medina, E.M. Medina Tovar, M. Ramirez Mejia, L. F. Coca, D. Diaz Escandon and M. Cardenas for assistance in the field in Colombia. We thank E. Muchnik, L. Konoreva and M. Zhurbenko for their help in obtaining specimens from Russia. We would like to thank Shuzo Oita (School of Plant Sciences, University of Arizona) and Prof. Yoshitaka Uchida (University of Hokkaido) for their help in organizing the logistics of the trip to Hokkaido and gathering all the permits, as well as Prof. Yoshitaka Uchida and all his students for help and assistance in the field. We would like to thank Prof. Karibu Fukuzawa (University of Hokkaido) and the Nakagawa Experimental Forest, and Prof. Ryunosuke Tateno (Kyoto University) and the Shibecha research forest for welcoming us and for assistance with the field studies in Hokkaido. Field trip in Japan in 2019 was supported by Fonds de la Recherche Scientifique - FNRS under grant number CDR J.0147.19. We would like to thank Prof. G. Thor for organizing the field trip to Nikko National park (Japan) in 2017. Permission for collection in Nikko National Park was kindly granted by the Nikko National Park management office, the Ministry of Environment (no. 1706215, 380, 381). We are thankful to N. Semenova and I. Zakhozhiy from Komi Scientific Center (Syktyvkar) for organizing the field trip to the Yugyd Va National Park (Komi Republic, Russia). Field trips in Taiwan (2016 and 2018) were made possible through strong support provided by the Endemic Species Research Institute, Jiji, Nantou Co in Taiwan 特有生物研究保育中心 especially advice and support in the field by Kuei-Yu Yao. Collection of Chilean species was made possible by the Chilean National Forest Corporation (CONAF) under permit 06/2014 to BG, and facilitated by Dr. Reinaldo Vargas (Universidad Metropolitana de Ciencias de la Educación, Santiago, Chile).

We thank E. Timdal, H. Holien, M. Bendiksby, T. Tønsberg and R. Haugan for the assistance with the field trip in Norway. We thank the GoLife team (mycophygolife.org), especially A. Elizabeth Arnold, József Geml and Alicia Ibánez, for the field support in Borneo and Panama, and the local collaborators, especially Dr. Monica Suleiman, for hosting us at University Malaysia Sabah (UMS) in Kota Kinabalu and for her generous help in obtaining legal documents. We also thank the UMS graduate students Foo She Fui and Mohd Hafiz Syukri for field assistance. We acknowledge the Sabah Biodiversity Center (SABC) and Sabah Parks for issuing collecting and export permits. The specimen from Borneo was collected by Nicolas Magain under SABC Access License JKM/MBS.1000-2/2 JLD.6 (101) and exported under Transfer License JKM/MB.1000-2/3 JLD.3 (70). We thank Stefan Ekman, Martin Westberg (UPS), Soili Stenroos, Leena Myllys (H), Michelle Price, Isabella Valette (G) for providing fragments of type specimens for DNA sequencing. We thank James Lendemer (NY), Stefan Ekman (UPS), Tor Tonsberg (BG) for accepting to divide original collections into holotype and isotype. We would like to thank South African National Parks (SANParks) for issuing our research permit (CRC/2019-2020/020–2018/V1) and to CapeNature for an export permit (CN17-31-9607). Many thanks to Dr. Terry Hedderson from University of Cape Town for hosting us and his invaluable help with organizing our visit to South Africa. We want to express our gratitude to the Panamanian Ministry of Environment for facilitating this research through issuing collecting and export permits; the Panamanian Institute for Scientific Research and High Technology Services (INDICASAT-AIP) for hosting the project and specifically Dr. Omar López for his assistance with the permitting process. We thank the Ministry of the Environment and the Ministry of Culture of Japan, the Daisetsuzan National Park and Shiretoko National Park and the Nakagawa city council for processing and delivering the collection permits. We thank Dr. Regine Fabri (Botanical Garden, Meise, Belgium) and Dr. Eva Holeèková (Institute of Botany of the CAS, Prùhonice, Czech Republic) for access to relevant publications. Field studies in several parts of Africa were made possible with the help and advice of local authorities and colleagues: for Madagascar, special thanks are due to Rogerlala Andriamiandrisoa, Eberhard Fischer, Damien Ertz, Dorothée Killmann and Tahina Razafindrahaja, the Missouri Botanical Garden offices at Antananarivo (in particular F. Lantoarisoa), the Parc Botanique et Zoologique de Tzimbazaza at Antananarivo and the Ministère de l’Environnement, de l’Ecologie et des Forêts; for Reunion, we wish to mention B. Lequette of the Parc National de La Réunion, and Claudine Ah-Peng and Dominique Starsberg of the University of La Réunion in Saint-Denis; for Rwanda, we wish to thank Bonny Dumbo, the Institut de Recherche Scientifique et Technologique (IRST) in Butare, the Office Rwandais du Tourisme et des Parcs Nationaux (ORTPN) and the Bureau de Jumelage Rhenanie Palatinat-Rwanda. For field work in Taiwan, we could rely on the expertise and guidance of Amber Isao and Kuei-Yu Yao of the Endemic Species Research Institute at Jiji for the permits (collection and export) and entrance and guidance in the National Parks. BG acknowledges support from NSF (DEB-0919284, DEB-1146295, DEB-1240045, DEB-1354631) for fieldwork in Chile and Taiwan. IG acknowledges support of the Estonian Research Council grant no. PSG884. Collecting from the Valdivian and the Cape Horn Region was made possible by CONAF and colleagues at Omora Ethnobotanical Park, and in particular Dr. Ricardo Rozzi, Dr. Francesca Massardo and Roy MacKenzie. PN and TW would like to thank Corporación Nacional Forestal (CONAF) for collecting permits in Chile and the herbarium at the University of Concepcion (CONC) for help with exporting specimens. We thank Laurent Gohy and Ido Cremasco in LG for technical assistance in the lab, as well as Maddie Paoletti for generating some sequences at DUKE. We thank Ian D. Medeiros (Duke University) for help with specimens and useful comments and discussion. We thank Einar Timdal, James Lendemer and an anonymous reviewer for their helpful comments and suggestions.

In compliance with Ecuadorian law and regulations the holotype specimens of *Peltigera massonii* and *Peltigera sipmanii* and epitype of *Peltigera pulverulenta* will be deposited in the mycological collection (fungario) of the Herbario Nacional del Ecuador (QCNE), in Quito, Ecuador. These specimens were collected by Camille Truong in Ecuador with research permit no. 008-07 IC-FLO-DNBAPVS/MA. We greatly appreciate the support by the curator of fungi MSc Rosa Batallas, Instituto Nacional de Biodiversidad (INABIO).

**Declaration on conflict of interest** The authors declare that there is no conflict of interest.

## REFERENCES

Ahti T, Vitikainen O. 1977. Notes on the lichens of Newfoundland. 5. Peltigeraceae. Annales Botanici Fennici 14: 89–94.

Aigoin DA, Devos N, Huttunen S, et al. 2009. And if Engler was not completely wrong? Evidence for multiple evolutionary origins in the moss flora of Macaronesia. Evolution 63: 3248–3257.

Alors D, Lumbsch HT, Divakar PK, et al. 2016. An integrative approach for understanding diversity in the Punctelia rudecta species complex (Parmeliaceae, Ascomycota). PLoS ONE 11(2): e0146537.

Aptroot A, Rodrigues AF, Schumm F, et al. 2010. Lista ds líquenes e fungos liquenícolas (Fungi). List of lichens and lichenicolous fungi (Fungi). In: Botges PAV et al. (eds), Listagem dos Organismos Terrestres e Marinhos dos Açores. A list of the Terrestrial and Marine Biota from the Azores. Princípia, Cascais: 59–79.

Aptroot A, Van de Vijver B, Lebouvier M, et al. 2011. Lichens of Ile Amsterdam and Ile Saint Paul (TAAF, southern Indian Ocean). Nova Hedwigia 92: 343–367.

Ariyawansa HA, Hawksworth DL, Hyde KD, et al. 2014 Epitypification and neotypification: guidelines with appropriate and inappropriate examples. Fungal Diversity 69: 57–91.

Armaleo D, Clerc P. 1991. Lichen chimeras: DNA analysis suggests that one fungus forms two morphotypes. Experimental Mycology 15: 1–10.

Arsenault A, Goward T. 2016. Macrolichen diversity as an indicator of stand age and ecosystem resilience along a precipitation gradient in humid forests of inland British Columbia, Canada. Ecological Indicators 69: 730–738.

Awasthi DD, Joshi M. 1982. Lichen genus Peltigera from India and Nepal. Kavaka 10: 47–62.

Bankevich A, Nurk S, Antipov D, et al. 2012. SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. Journal of Computational Biology 19: 455–477.

Bazzicalupo AL, Buyck B, Saar I, et al. 2017. Troubles with mycorrhizal mushroom identification where morphological differentiation lags behind barcode divergence. Taxon 66: 791–810.

Bengtsson-Palme J, Ryberg M, Hartmann M, et al. 2013. Improved software detection and extraction of ITS1 and ITS 2 from ribosomal ITS sequences of fungi and other eukaryotes for analysis of environmental sequencing data. Methods in Ecology and Evolution 4: 914–919.

Bolger AM, Lohse M, Usadel B. 2014. Trimmomatic: a flexible trimmer for Illumina sequence data. Bioinformatics 30: 2114–2120.

Boluda CG, Rico VJ, Divakar PK, et al. 2019. Evaluating methodologies for species delimitation: the mismatch between phenotypes and genotypes in lichenized fungi (Bryoria sect. Implexae, Parmeliaceae). Persoonia 42: 75–100.

Cannon P, Magain N, Sérusiaux E, et al. 2021. Peltigerales: Peltigeraceae, including the genera Crocodia, Lobaria, Lobarina, Nephroma, Peltigera, Pseudocyphellaria, Ricasolia, Solorina and Sticta. Revisions of British and Irish Lichens 20: 1–34.

Carbone I, White JB, Miadlikowska J, et al. 2019. T-BAS version 2.1: Tree-Based Alignment Selector toolkit for evolutionary placement and viewing of alignments and metadata on curated and custom trees. Microbiology Resource Announcements 8: e00328-19.

Chagnon PL, Magain N, Miadlikowska J, et al. 2018. Strong specificity and network modularity at a very fine phylogenetic scale in the lichen genus Peltigera. Oecologia 187: 767–782.

Chagnon PL, Magain N, Miadlikowska J, et al. 2019. Species diversification and phylogenetically constrained symbiont switching generated high modularity in the lichen genus Peltigera. Journal of Ecology 107: 1645–1661.

Clarke D. 2016. Peltigera hymenina: a taxonomic enigma. British Lichen Society Bulletin 118: 6–7.

Coca LF, Lücking R. 2016. A first attempt at a global phylogenetic revision of the genus Coccocarpia (Ascomycota: Peltigerales). Abstract book, The 8th IAL Symposium, Helsinki, Finland: 63.

Darnajoux R, Constantin J, Miadlikowska J, et al. 2014. Is vanadium a biometal for boreal cyanolichens? New Phytologist 202: 765–771.

Darnajoux R, Lutzoni F, Miadlikowska J, et al. 2015. Determination of elemental baseline using peltigeralean lichens from Northeastern Canada (Québec): Initial data collection for long term monitoring of the impact of global climate change on boreal and subarctic area in Canada. Science of the Total Environment 533: 1–7.

Darnajoux R, Magain N, Renaudin M, et al. 2019. Molybdenum threshold for ecosystem scale alternative vanadium nitrogenase activity in boreal forests. Proceedings of the National Academy of Sciences 116: 24682–24688.

Darnajoux R, Zhang X, McRose DL, et al. 2017. Biological nitrogen fixation by alternative nitrogenases in boreal cyanolichens: importance of molybdenum availability and implications for current biological nitrogen fixation estimates. New Phytologist 213: 680–689.

De Queiroz K. 2005. Different species problems and their resolution. BioEssays 27: 1263–1269.

De Queiroz K. 2007. Species concepts and species delimitation. Systematic Biology 56: 879–886.

Del-Prado R, Divakar PK, Lumbsch HT, et al. 2016. Hidden genetic diversity in an asexually reproducing lichen forming fungal group. PLoS ONE 11: e0161031.

Díaz EM, Vicente-Manzanares M, Legaz ME, et al. 2015. A cyanobacterial ß-actin-like protein, responsible for lichenized Nostoc sp. motility towards a fungal lectin. Acta Physiologiae Plantarum 37: 249.

Dillman KL, Ahti T, Björk CR, et al. 2012. New records, range extensions and nomenclatural innovations for lichens and lichenicolous fungi from Alaska, USA. Herzogia 25: 177–210.

Ekman S, Wedin M, Lindblom K, et al. 2014. Extended phylogeny and a revised generic classification of the Pannariaceae (Peltigerales, Ascomycota). The Lichenologist 46: 627–656.

Elix JA. 2014. A catalogue of standardized chromatographic data and biosynthetic relationships for lichen substances. Third Edition, published by the author, Canberra. Accessible at https://www.anbg.gov.au/abrs/lichenlist/Chem%20Cat%203.pdf.

Elix JA. 2016. Seven new species of Buellia sens.lat. (Ascomycota, Physciaceae) from southern mainland Australia. Australasian Lichenology 78: 32–45.

Elix JA, McCarthy PM. 1998. Catalogue of the lichens of the smaller Pacific Islands. Bibliotheca Lichenologica 70: 1–361.

Ence DD, Carstens BC. 2011. SpedeSTEM: a rapid and accurate method for species delimitation. Molecular Ecology Resources 11: 473–480.

Galloway DJ. 1985. Flora of New Zealand Lichens. P.D. Hasselberg, Government Printer, Wellington.

Galloway DJ. 2000. The lichen genus Peltigera (Peltigerales: Ascomycota) in New Zealand. Tuhinga 11: 1–45.

Galloway DJ. 2007. Flora of New Zealand lichens. Revised second edition including lichen-forming and lichenicolous fungi. Volumes 1 and 2. Manaaki Whenua Press, Lincoln, New Zealand.

Galloway DJ, Quilhot W. 1998. Checklist of Chilean lichen-forming and lichenicolous fungi. Gayana Botanica 55: 111–185.

Gasparyan A, Sipman HJ, Lücking R. 2017. Ramalina europaea and R. labiosorediata, two new species of the R. pollinaria group (Ascomycota: Ramalinaceae), and new typifications for Lichen pollinarius and L. squarrosus. The Lichenologist 49: 301–319.

Goffinet B, Bayer RJ. 1997. Characterization of mycobionts of photomorph pairs in the Peltigerineae (Lichenized Ascomycetes) based on Internal Transcribed Spacer sequences of the nuclear ribosomal DNA. Fungal Genetics and Biology 21: 228–237.

Goffinet B, Hastings RI. 1994. The lichen genus Peltigera (Lichenized Ascomycetes) in Alberta. Natural History Occasional Paper 21: i–vi, 1–54.

Goffinet B, Miadlikowska J. 1999. Peltigera phyllidiosa (Peltigeraceae, ascomycotina), a new species from the Southern Appalachians corroborated by its sequences. The Lichenologist 31: 247–256.

Goffinet B, Miadlikowska J, Goward T. 2003. Phylogenetic inferences based on nrDNA sequences support five morphospecies within the Peltigera didactyla complex (Lichenized Ascomycota). The Bryologist 106: 349–364.

Goffinet B, Sérusiaux E, Diederich P. 1994. Le genre Peltigera (Lichenes) en Belgique et au Grand-Duché de Luxembourg. Belgian Journal of Botany 127: 184–206.

Goward T, Arsenault A. 2000. Cyanolichens and conifers: implications for global conservation. Forest Snow and Landscape Research 75: 303–318.

Goward T, Goffinet B, Vitikainen O. 1995. Synopsis of the genus Peltigera (lichenized Ascomycetes) in British Columbia, with a key to the North American species. Canadian Journal of Botany 73: 91–111.

Grube M, Berg G, Andrésson ÓS, et al. 2014. Lichen genomics: prospects and progress. In: Martin F (ed), The ecological genomics of fungi: 191–212. John Wiley & Sons, Inc, Hoboken, NJ, USA.

Gyelnik V. 1927a. Peltigera tenulmányok, Peltigera-Studien. Botanikai Közlemények 24: 122–141.

Gyelnik V. 1927b. Lichenologiai Közlemények, Lichenologische Mitteilungen 1–3. Magyar Botanikai Lapok 26: 45–47.

Gyelnik V. 1931. Notes on Peltigera. The Bryologist 34: 16–19.

Gyelnik V. 1932. Peltigerae novae et rarae. Annales de Cryptogamie Exotique 5: 39–40.

Gyelnik V. 1933. Clavis et enumeratio lichenum europaeorum novorum rariorumque. Revue Bryologique et Lichénologique 5: 61–73.

Gyelnik V. 1936. Revisio typorum ab auctoribus variis descriptorum II. Annales historico-naturales musei nationalis hungarici. Pars Botanica 30: 119–135.

Hafellner J, Türk R. 2001. Die lichenisierten Pilze Österreichs - eine Checkliste der bisher nachgewiesenen Arten mit Verbreitungsangaben. Stapfia 76: 1–167

Han LF, Xu XM, Yang JY, et al. 2018. Peltigera neodegenii sp. nov. from Central China. Mycotaxon 133: 323–332.

Han LF, Yang JY, Bei SQ, et al. 2019. Peltigera shennongjiana, a new cyanolichen from Central China. The Lichenologist 51: 561–574.

Han LF, Zhang YY, Guo SY. 2013. Peltigera wulingensis, a new lichen (Ascomycota) from North China. The Lichenologist 45: 329–336.

Han LF, Zheng TX, Guo SY. 2015. A new species in the lichen genus Peltigera from northern China based on morphology and DNA sequence data. The Bryologist 118: 46–53.

Hawksworth DL. 1974. Mycologist's handbook. Commonwealth Mycological Institute, Kew, Surrey, U.K.

Hodkinson BP, Allen JL, Forrest L, et al. 2014. Lichen-symbiotic cyanobacteria associated with Peltigera have an alternative vanadium-dependent nitrogen fixation system. European Journal of Phycology 49: 11–19

Holtan-Hartwig J. 1993. The lichen genus Peltigera, exclusive of the P. canina group, in Norway. Sommerfeltia 15: 1–77.

Huelsenbeck JP, Andolfatto P, Huelsenbeck ET. 2011. Structurama: Bayesian inference of population structure. Evolutionary Bioinformatics 7: EBO-S6761.

Inumaru S. 1943. Studia Lichenum Japoniae. III. Peltigeraceae Japoniae III. Acta Phytotaxonomica et Geobotanica 12: 1–16.

Izuno A, Hatakeyama M, Nishiyama T, et al. 2016. Genome sequencing of Metrosideros polymorpha (Myrtaceae), a dominant species in various habitats in the Hawaiian Islands with remarkable phenotypic variations. Journal of Plant Research 129: 727–736.

Jørgensen PM. 1977. Foliose and fruticose lichens from Tristan da Cunha. Det Norske Videnskap-Akademi, I. Mat.-Naturv. Klasse Skrifter, Ny Serie n° 36: 1–40.

Jüriado I, Kaasalainen U, Jylhä M, et al. 2019. Relationships between mycobiont identity, photobiont specificity and ecological preferences in the lichen genus Peltigera (Ascomycota) in Estonia (northeastern Europe). Fungal Ecology 39: 45–54.

Jüriado I, Kaasalainen U, Rikkinen J. 2017. Specialist taxa restricted to threatened habitats contribute significantly to the regional diversity of Peltigera (Lecanoromycetes, Ascomycota) in Estonia. Fungal Ecology 30: 76–87.

Kaasalainen U, Biermann L, Mollel NP, et al. 2022. Peltigera (Lecanoromycetes) on Mt Kilimanjaro, East Africa. The Lichenologist, 54(5): 231–243.

Kampa A, Gagunashvili AN, Gulder TAM, et al. 2013. Metagenomic natural product discovery in lichen provides evidence for a family of biosynthetic pathways in diverse symbioses. Proceedings of the National Academy of Sciences 110: E3129–E3137.

Kashiwadani H, Inoue M. 1993. The lichens of Kushiro Marsh, Hokkaido, Japan. Memoirs of the National Science Museum [Tokyo] 26: 53–66.

Kõljalg U, Nilsson RH, Abarenkov K, et al. 2013. Towards a unified paradigm for sequence-based identification of fungi. Molecular Ecology 22: 5271–5277.

Kondraskov P, Schütz N, Schüßler C, et al. 2015. Biogeography of Mediterranean hotspot biodiversity: Re-evaluating the 'Tertiary Relict' hypothesis of Macaronesian laurel forests. PLoS One 19(7): e0132091.

Kristinsson H. 1968. Peltigera occidentalis in Iceland. The Bryologist 71: 38–40.

Kukwa M, Sipman HJM, Etayo X, et al. 2014. The lichen order Peltigerales in Bolivia – The first assessment of the biodiversity. Herzogia 27: 321–345.

Kurokawa S (ed). 2003. Checklist of Japanese lichens. National Science Museum Tokyo, Japan.

Kurokawa S, Kashiwadani H. 2006. Checklist of Japanese lichens and allied fungi. National Science Museum Monographs 33: 1–157.

Lanfear R, Calcott B, Ho SY, et al. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29: 1695–1701.

Lanfear R, Frandsen PB, Wright AM, et al. 2016. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular Biology and Evolution 34: 772–773.

Laundon JR. 1984. The typification of Withering's neglected lichens. The Lichenologist 16: 211–239.

Leavitt SD, Divakar PK, Crespo A, et al. 2016a. A matter of time – understanding the limits of the power of molecular data for delimiting species boundaries. Herzogia 29: 479–492.

Leavitt SD, Esslinger TL, Divakar PK, et al. 2016b. Hidden diversity before our eyes: Delimiting and describing cryptic lichen-forming fungal species in camouflage lichens (Parmeliaceae, Ascomycota). Fungal Biology 120: 1374–1391.

Leavitt SD, Kirika PM, De Paz GA, et al. 2018. Assessing phylogeny and historical biogeography of the largest genus of lichen-forming fungi, Xanthoparmelia (Parmeliaceae, Ascomycota). The Lichenologist 50: 299–312.

Leiva D, Fernández-Mendoza F, Acevedo J, et al. 2021. The bacterial community of the foliose macro-lichen Peltigera frigida is more than a mere extension of the microbiota of the subjacent substrate. Microbial Ecology 81: 965–976.

Lendemer JC. 2011. A taxonomic revision of the North American species of Lepraria s.lat. that produce divaricatic acid, with notes on the type species of the genus L. incana. Mycologia 103: 1216–1229.

Lendemer JC. 2020. Epitypes are forever: Best practices for an increasingly misused nomenclatural action. Taxon 69: 849–850.

Lendemer JC, O'Brien HE. 2011. How do you reconcile molecular and non-molecular datasets? A case study where new molecular data prompts a revision of Peltigera hydrothyria s.lat. in North America and the recognition of two species. Opuscula Philolichenum 9: 99–110.

Li L, Li J, Rohwer JG, et al. 2011. Molecular phylogenetic analysis of the Persea group (Lauraceae) and its biogeographic implications on the evolution of tropical and subtropical Amphi-Pacific disjunctions. American Journal of Botany 98: 1520–1536.

Linnaeus C. 1753. Species Plantarum Volume II: 1149.

Louwhoff S. 2008. New and additional records and a new combination of Australian Peltigera. Australasian Lichenology 63: 40–46.

Louwhoff S. 2009. Peltigeraceae. In: McCarthy PM (ed), Flora of Australia Volume 57, Lichens 5: 428–446. ABRS and CSIRO Publishing, Canberra and Melbourne, Australia.

Lu J, Magain N, Miadlikowska J, et al. 2018. Bioclimatic factors at an intra-biome scale are more limiting than cyanobiont availability for the lichen-forming genus Peltigera. American Journal of Botany 105: 1198–1211.

Lücking R. 2020. Three challenges to contemporaneous taxonomy from a licheno-mycological perspective. Megataxa 1: 78–103.

Lücking R, Cáceres ME, Silva NG, et al. 2015. The genus Cora in the South Atlantic and the Mascarenes: Two novel taxa and inferred biogeographic relationships. The Bryologist 118: 293–304.

Lücking R, Hodkinson BP, Leavitt SD. 2017a. The 2016 classification of lichenized fungi in the Ascomycota and Basidiomycota – approaching one thousand genera. The Bryologist 119: 361–416.

Lücking R, Moncada B, McCune B, et al. 2017b. Pseudocyphellaria crocata (Ascomycota: Lobariaceae) in the Americas is revealed to be thirteen species, and none of them is P. crocata. The Bryologist 120: 441–500.

Lücking R, Moncada B, Widhelm TJ, et al. 2021. The Sticta filix-Sticta lacera conundrum (lichenized Ascomycota: Peltigeraceae subfamily Lobarioideae): unresolved lineage sorting or developmental switch? Botanical Journal of the Linnean Society 199: 706–727.

Lücking R, Sérusiaux E, Maia LC, et al. 1998. A revision of the names of foliicolous lichenized fungi published by Batista and co-workers between 1960 and 1975. The Lichenologist 30: 121–191.

Lumbsch HT, Leavitt SD. 2011. Goodbye morphology? A paradigm shift in the delimitation of species in lichenized fungi. Fungal Diversity 50: 59–72.

Magain N, Goffinet B, Sérusiaux E. 2012. Further photomorphs in the lichen family Lobariaceae from Reunion (Mascarene archipelago) with notes on the phylogeny of Dendriscocaulon cyanomorphs. The Bryologist 115: 243–254.

Magain N, Goffinet B, Simon A, et al. 2020. Peltigera serusiauxii (Lecanoromycetes, Ascomycota), a new species from Papua New Guinea and Malaysia. Plant and Fungal Systematics 65: 139–146.

Magain N, Miadlikowska J, Goffinet B, et al. 2017a. Evolution of specificity in fungi-cyanobacteria symbioses: a case study in Peltigera section Polydactylon (lichenized Ascomycota; Peltigerales). Systematic Biology 66: 74–99.

Magain N, Miadlikowska J, Mueller O, et al. 2017b. Conserved genomic collinearity as a source of broadly applicable, fast evolving, markers to resolve species complexes: a case study using the lichen-forming genus Peltigera section Polydactylon. Molecular Phylogenetics and Evolution 117: 10–29.

Magain N, Sérusiaux E. 2014. Do photobiont switch and cephalodia emancipation act as evolutionary drivers in the lichen symbiosis? A case study in the Pannariaceae (Peltigerales). PLoS ONE 9: e8987.

Magain N, Sérusiaux E. 2015a. Dismantling the treasured flagship lichen Sticta fuliginosa (Peltigerales) into four species in Western Europe. Mycological Progress 14: 97.

Magain N, Sérusiaux E. 2015b. The lichen genus Kroswia is a synonym of Fuscopannaria (Pannariaceae). The Lichenologist 47: 35–42.

Magain N, Sérusiaux E, Zhurbenko MP, et al. 2016. Disentangling the Peltigera polydactylon species complex by recognizing P. polydactylon subsp. udeghe and P. seneca. Herzogia 29: 514–528.

Magain N, Truong C, Goward T, et al. 2018. 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). Taxon 67: 836–870.

Magnusson AH, Zahlbruckner A. 1943. Hawaiian lichens I. The families Verrucariaceae to Peltigeraceae. Arkiv för Botanik 31A: 1–96.

Manoharan-Basil SS, Miadlikowska J, Goward T, et al. 2016. Peltigera islandica, a new cyanolichen species in section Peltigera ('P. canina group'). The Lichenologist 48: 451–467.

Martínez I, Burgaz AR. 1997. Additions to the chemistry, ecology and distribution of Peltigera melanorrhiza and P. neopolydactyla. Mycotaxon 63: 389–394.

Martinez I, Burgaz AR, Vitikainen O. 1997. Studies on the genus Peltigera in the Iberian Peninsula. II. Nova Hedwigia 64: 367–391.

Martínez I, Burgaz AR, Vitikainen O, et al. 2003. Distribution patterns in the genus Peltigera Willd. The Lichenologist 35: 301–323.

McCune B, Geiser L. 2009. Macrolichens of the Pacific Northwest. Second Edition. Oregon State University Press, Corvallis, OR, USA.

McMullin RT, Miadlikowska J. 2022. Two rare Peltigera species new to the Canadian Arctic, P. islandica and P. lyngei. Plant and Fungal Systematics 67:17–23.

Miadlikowska J, Lutzoni F. 2000. Phylogenetic revision of the genus Peltigera (lichen-forming Ascomycota) based on morphological, chemical, and large subunit nuclear ribosomal DNA data. International Journal of Plant Sciences 161: 925–958.

Miadlikowska J, Lutzoni F. 2004. Phylogenetic classification of peltigeralean fungi (Peltigerales, Ascomycota) based on ribosomal RNA small and large subunits. American Journal of Botany 91: 449–464.

Miadlikowska J, Lutzoni F, Goward T, et al. 2003. New approach to an old problem: incorporating signal from gap-rich regions of ITS and rDNA large subunit into phylogenetic analyses to resolve the Peltigera canina species complex. Mycologia 95: 1181–1203.

Miadlikowska J, Magain N, Buck WR, et al. 2020 Peltigera hydrophila (Lecanoromycetes, Ascomycota), a new semi-aquatic cyanolichen species from Chile. Plant and Fungal Systematics 65: 210–218.

Miadlikowska J, Magain N, Pardo-De la Hoz CJ, et al. 2018. Species in section Peltidea (aphthosa group) of the genus Peltigera remain cryptic after molecular phylogenetic revision. Plant and Fungal Systematics 63: 45–64.

Miadlikowska J, McCune B, Lutzoni F. 2002. Pseudocyphellaria perpetua, a new lichen from Western North America. The Bryologist 105: 1–10.

Miadlikowska J, Richardson D, Magain N, et al. 2014. Phylogenetic placement, species delimitation, and cyanobiont identity of endangered aquatic Peltigera species (lichen-forming Ascomycota, Lecanoromycetes). American Journal of Botany 101: 1141–1156.

Miao VPW, Manoharan SS, Snæbjarnarson V, et al. 2012. Expression of lec-1, a mycobiont gene encoding a galectin-like protein in the lichen Peltigera membranacea. Symbiosis 57: 23–31.

Miller MA, Pfeiffer W, Schwartz T. 2010 (November). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Gateway Computing Environments Workshop (GCE), 2010: 1–8. New Orleans, LA.

Molina MC, Divakar PK, Millanes AM, et al. 2011. Parmelia sulcata (Ascomycota: Parmeliaceae), a sympatric monophyletic species complex. The Lichenologist 43: 585–601.

Moncada B, Coca LF, Lücking R. 2013a. Neotropical members of Sticta (lichenized Ascomycota: Lobariaceae) forming photosymbiodemes, with the description of seven new species. The Bryologist 116: 169–200.

Moncada B, Lücking R, Betancourt-Macuase L. 2013b. Phylogeny of the Lobariaceae (lichenized Ascomycota: Peltigerales), with a reappraisal of the genus Lobariella. The Lichenologist 45: 203–263.

Moncada B, Lücking R, Suárez A. 2014a. Molecular phylogeny of the genus Sticta (lichenized Ascomycota: Lobariaceae) in Colombia. Fungal Diversity 64: 205–231.

Moncada B, Reidy B, Lücking R. 2014b. A phylogenetic revision of Hawaiian Pseudocyphellaria sensu lato (lichenized Ascomycota: Lobariaceae) reveals eight new species and a high degree of inferred endemism. The Bryologist 117: 119–160.

Nifontova MG. 1996. Mushrooms, lichens and mosses as biological indicators of radioactive environmental contamination. In: Luykx FF, Frissel MJ (eds), Radioecology and the restoration of radioactive-contaminated sites: 155–162. Springer, Netherlands.

Nimis PL, Hafellner J, Roux C, et al. 2018. The lichens of the Alps – an annotated checklist. MycoKeys 31: 1–634.

Nordén B, Paltto H, Götmark F, et al. 2007. Indicators of biodiversity, what do they indicate? Lessons for conservation of cryptogams in oak-rich forest. Biological Conservation 135: 369–379.

Nylander W. 1886. Lichenes Insulae Sancti Pauli. Flora 69: 318–322.

O'Brien HE, Miadlikowska J, Lutzoni F. 2009. Assessing reproductive isolation in highly diverse communities of the lichen-forming fungal genus Peltigera. Evolution 63: 2076–2086.

O'Brien HE, Miadlikowska J, Lutzoni F. 2013. Assessing population structure and host specialization in lichenized cyanobacteria. New Phytologist 198: 557–566.

Ohmura Y, Kashiwadani H. 1997. Lichens of Mt. O-akan and its adjacent areas, Hokkaido, Japan. Bulletin of the National Science Museum (Tokyo), Series B (Botany) 23: 1–24.

Olson DM, Dinerstein E, Wikramanayake ED, et al. 2001. Terrestrial ecoregions of the world: A new map of life on earth. A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. BioScience 51: 933–938.

Onuţ-Brännström I, Tibell L, Johannesson H. 2017. A worldwide phylogeography of the whiteworm lichens Thamnolia reveals three lineages with distinct habitats and evolutionary histories. Ecology and Evolution 7(10): 3602–3615.

Orange A, James PW, White FJ. 2010. Microchemical methods for the identification of lichens. British Lichen Society, London.

Otálora MAG, Martínez I, Aragón G, et al. 2017. Species delimitation and phylogeography of the Pectenia species-complex: A misunderstood case of species-pairs in lichenized fungi, where reproduction mode does not delimit lineages. Fungal Biology 21: 222–233

Ott S. 1988. Photosymbiodemes and their development in Peltigera venosa. The Lichenologist 20: 361–368.

Pardo-De la Hoz CJ, Magain N, Lutzoni F, et al. 2018. Contrasting symbiotic patterns in two closely related lineages of trimembered lichens of the genus Peltigera. Frontiers in Microbiology 9: 2770.

Pino-Bodas R, Burgaz AR, Martín MP, et al. 2015. The phenotypic features used for distinguishing species within the Cladonia furcata complex are highly homoplasious. The Lichenologist 47: 287–303.

Pino-Bodas R, Martín MP, Burgaz AR, et al. 2013. Species delimitation in Cladonia (Ascomycota): A challenge to the DNA barcoding philosophy. Molecular Ecology Resources 13: 1058–1068.

Purvis OW, James PW. 1993. Studies in the lichens of the Azores. Part 1. Caldeira do Faial. Arquipélago 11A: 1–15.

Radies D, Coxson D, Johnson C, et al. 2009. Predicting canopy macrolichen diversity and abundance within old-growth inland temperate rainforests. Forest Ecology and Management 259: 86–97.

Ramírez-Fernández L, Carú M, Yahr R, et al. 2015. Phylogenetic diversity of Peltigera cyanolichens and their photobionts in Southern Chile and Antarctica. Microbes and Environments 30: 172–179.

Rannala B. 2015. The art of science of species delimitation. Current Zoology 61: 846–853.

Reid NM, Carstens BC. 2012. Phylogenetic estimation error can decrease the accuracy of species delimitation: a Bayesian implementation of the general mixed Yule-coalescent model. BMC Evolutionary Biology 12: 1–11.

Renner SA. 2016. Return to Linnaeus's focus on diagnosis, not description: the use of DNA characters in the formal naming of species. Systematic Biology 65: 1085–1095.

Rodríguez FJLOJ, Oliver JL, Marin A, et al. 1990. The general stochastic model of nucleotide substitution. Journal of Theoretical Biology 142: 485–501.

Roux C, Monnat JY, Van Haluwyn C, et al. 2014. Catalogue des lichens et champignons lichénicoles de France métropolitaine. 2e édition revue et augmentée. Association française de lichénologie (AFL), Fougères: Henry des Abbayes, Fontainebleau, France.

Saag L, Mark K, Saa A, et al. 2014. Species delimitation in the lichenized fungal genus Vulpicida (Parmeliaceae, Ascomycota) using gene concatenation and coalescent-based species tree approaches. American Journal of Botany 101: 2169–2182.

Schoch CL, Seifert KA, Huhndorf S, et al. 2012. Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. Proceedings of the National Academy of Sciences 109: 6241–6246.

Seaward MRD. 2002. Lichens as monitors of radioelements. In: Nimis PL, Scheidegger C, Wolseley PA (eds), Monitoring with Lichens – Monitoring Lichens: 85–96. Springer, Netherlands.

Sérusiaux E, Goffinet B, Miadlikowska J, et al. 2009. Taxonomy, phylogeny and biogeography of the lichen genus Peltigera in Papua New Guinea. Fungal Diversity 38: 185–224.

Sérusiaux E, Villarreal AJC, Wheeler T, et al. 2011. Recent origin, active speciation and dispersal for the lichen genus Nephroma (Peltigerales) in Macaronesia. Journal of Biogeography 38: 1138–1151.

Shiba T, Moon KH, Kashiwadani H. 2008. Lichens of Akkeshi and its adjacent areas, northeastern Hokkaido, Japan. Bulletin of the National Science Museum, Tokyo, Series B 34: 1–16.

Simon A, Goffinet B, Magain N, et al. 2018. High diversity, high insular endemism and recent origin in the lichen genus Sticta (lichenized Ascomycota, Peltigerales) in Madagascar and the Mascarenes. Molecular Phylogenetics and Evolution 122: 15–28.

Spjut R, Simon A, Guissard M, et al. 2020. The fruticose genera in the Ramalinaceae (Ascomycota, Lecanoromycetes): their diversity and evolutionary history. MycoKeys 73: 1–68.

Spribille T, Björk CR, Ekman S, et al. 2009. Contributions to an epiphytic lichen flora of northwest North America: I. Eight new species from British Columbia inland rain forests. The Bryologist 112: 109–137.

Stacy EA, Johansen JB, Sakishima T, et al. 2014. Incipient radiation within the dominant Hawaiian tree Metrosideros polymorpha. Heredity 113: 334–342.

Stacy EA, Paritosh B, Johnson MA, et al. 2017. Incipient ecological speciation between successional varieties of a dominant tree involves intrinsic postzygotic isolating barriers. Ecology and Evolution 7: 2501–2512.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688–2690.

Stamatakis A, Hoover P, Rougemont J. 2008. A rapid bootstrap algorithm for the RAxML web servers. Systematic Biology 57: 758–771.

Steinhäuser SS, Andrésson ÓS, Pálsson A, et al. 2016. Fungal and cyanobacterial gene expression in a lichen symbiosis: Effect of temperature and location. Fungal Biology 120: 1194–1208.

Swinscow TDV, Krog H. 1988. Macrolichens of East Africa. British Museum (Natural History), London, UK.

Takhtajan A, Crovello TJ, Cronquist A. 1986. Floristic regions of the world (Vol. 544). University of California press, Berkeley, CA, USA.

Timdal E, Rui S. 2021. Peltigera seneca new to Europe. Graphis Scripta 33: 79–85.

Tønsberg T. 1999. Pseudocyphellaria arvidssonii new to Africa and P. mallota new to North America. The Bryologist 102: 128–129.

Tønsberg T, Holtan-Hartwig J. 1983. Phycotype pairs in Nephroma, Peltigera and Lobaria in Norway. Nordic Journal of Botany 3: 681–688.

Tripp EA, Lendemer JC. 2014. Sleepless nights: When you can't find anything to use but molecules to describe new taxa. Taxon 63: 969–971.

Tuhkanen S. 1984. A circumboreal system of climatic-phytogeographical regions. Acta Botanica Fennica 127: 1–50.

Turland NJ, Wiersema JH, Barrie FR, et al. 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Coe) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten, Germany.

Vallese C, Nascimbene J, Giordani P, et al. 2021. Modelling range dynamics of terricolous lichens of the genus Peltigera in the Alps under a climate change scenario. Fungal Ecology 49: 101014.

Vitikainen O. 1985. Three new species of Peltigera (lichenized Ascomycetes). Annales Botanici Fennici 22: 291–298.

Vitikainen O. 1994a. Taxonomic revision of Peltigera (lichenized Ascomycotina) in Europe. Acta Botanica Fennica 152: 1–96.

Vitikainen O. 1994b. Notes on some Peltigera of the Neotropics. Acta Botanica Fennica 150: 217–221.

Vitikainen O. 1995. Peltigera andensis sp. nov. (Peltigeraceae, lichenized Ascomycetes), a new species from South America. In: Daniëls FJA, Schulz M, Peine J (eds), Flechten Follmann. Contributions to lichenology in Honour of Gerhard Follmann: 371–375. Geobotanical and Phytotaxonomical Study Group, Botanical Institute, University of Cologne, Cologne, Germany.

Vitikainen O. 1998. Taxonomic notes on neotropical species of Peltigera. In: Marcelli MP, Seaward MRD (eds), Lichenology in Latin America: History, current knowledge and applications: 135–139. CETESB, Companhia de Tecnologia de Saneamento Ambiental, Estado de Sao Paulo, Sao Paulo, Brazil.

Vitikainen O. 2002. Notes on Peltigera (Peltigeraceae) in southern South America and Antarctic regions. Mitteilungen aus dem Institut für Allgemeine Botanik in Hamburg 30-32: 297–303.

Vitikainen O. 2004. Peltigera. In: Nash TH III, Ryan BD, Diederich P, et al. (eds), Lichen Flora of the Greater Sonoran Desert Region, Vol. 2: 389–399. Lichens Unlimited, Arizona State University, Tempe, Arizona, USA.

Vitikainen O. 2007. Peltigeraceae. In: Ahti T, Stenroos S (eds), Nordic Lichen Flora. Volume 3. Cyanolichens: 113–131. Nordic Lichen Society, Uddevalla, Sweden.

Wei XL, Wang XY, Koh YJ, et al. 2009. Taxonomic study of Peltigera (Peltigeraceae, Ascomycota) in Korea. Mycobiology 37: 189–196.

Willdenow KL. 1787. Florae berolinensis prodromus. Vieweg.

Wirth V, Hauck M, Schultz M. 2013. Die Flechten Deutschlands, Band 2: 677–1244. Ulmer, Stuttgart, Germany.

Xavier BB, Miao VP, Jónsson ZO, et al. 2012. Mitochondrial genomes from the lichenized fungi Peltigera membranacea and Peltigera malacea: features and phylogeny. Fungal Biology 116: 802–814.

Yang Z, Rannala B. 2010. Bayesian species delimitation using multilocus sequence data. Proceedings of the National Academy of Sciences 107: 9264–9269.

Yang Z, Rannala B. 2014. Unguided species delimitation using DNA sequence data from multiple loci. Molecular Biology and Evolution 31: 3125–3135.

Zhang J, Kapli P, Pavlidis P, et al. 2013. A general species delimitation method with applications to phylogenetic placements. Bioinformatics 29: 2869–2876.

Zheludeva EV. 2017. New records of lichen species from Magadan region. Turczaninowia 20: 64–74.

### Supplementary material

**Fig. S1** TLC in phase C for representatives of the *dolichorhiza* group. See Table S2 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

**Fig. S2** TLC in phase C for representatives of the *dolichorhiza* and *hymenina* groups. See Table S2 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

**Fig. S3** TLC in phase C for representatives of *P. truculenta* (incl. var. *austroscabrosa*). See Table S2 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

**Fig. S4** TLC in phase C for representatives of *Peltigera hawaiiensis* and *P. gallowayi*. See Table S2 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

**Fig. S5** TLC in phase C for representatives of the *hymenina* group. See Table S2 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

**Fig. S6** TLC in phase C for representatives of the *pacifica* group. See Table S2 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

**Fig. S7** TLC in phase C for representatives of the *pacifica* group and *occidentalis* subclade. See Table S2 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

**Fig. S8** TLC in phase C for representatives of the *occidentalis*, *scabrosella* and *melanorrhiza* subclades. See Table S2 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

**Fig. S9** TLC in phase C for representatives of the *melanorrhiza* and *scabrosa* subclades. See Table S2 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

**Fig. S10** TLC in phase C for representatives of the *scabrosa* subclade. See Table S2 for detailed voucher information. D = dolichorrhizin, G = gyrophoric acid, M = methylgyrophorate, P = peltidactylin, T = tenuiorin, Z = zeorin. See Material and Methods for details.

**Fig. S11** Type specimen of *Peltigera meridiana.*

**Table S1** Voucher information for specimens included in the TLC plates shown in Fig. 37–43, along with detected substances for each specimen, and summary of detected substances for each species.

**Table S2** Voucher information for specimens included in the TLC plates shown in Fig. S2–S11.