

Taxonomy, phylogeny and biogeography of the lichen genus *Peltigera* in Papua New Guinea

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Sérusiaux, E., Goffinet, B., Miadlikowska, J. and Vitikainen, O. (2009). Taxonomy, phylogeny and biogeography of the the lichen genus *Peltigera* in Papua New Guinea. *Fungal Diversity* 38: 185-224.

The lichen genus *Peltigera* is represented in Papua New Guinea by 15 species, including 6 described as new for science: *P. cichoracea*, *P. didactyla*, *P. dolichorhiza*, *P. erioderma*, *P. extenuata*, *P. fimbriata* sp. nov., *P. granulosa* sp. nov., *P. kopenhagenii* sp. nov., *P. montis-wilhelmii* sp. nov., *P. nana*, *P. oceanica*, *P. papuana* sp. nov., *P. sumatrana*, *P. ulcerata*, and *P. weberi* sp. nov. *Peltigera macra* and *P. tereziana* var. *philippinensis* are reduced to synonymy with *P. nana*, whereas *P. melanocoma* is maintained as a species distinct from *P. nana* pending further studies. The status of several putative taxa referred to *P. dolichorhiza* s. lat. in the Sect. *Polydactylon* remains to be studied on a wider geographical scale and in the context of *P. dolichorhiza* and *P. neopolydactyla*. The phylogenetic affinities of all but one regional species (*P. extenuata*) are studied based on inferences from ITS (nrDNA) sequence data, in the context of a broad taxonomic sampling within the genus. A key to all species is provided and available data on their ecology and general distribution are discussed. The species *P. canina*, *P. horizontalis*, *P. laciniata*, *P. malacea*, *P. polydactylon* and *P. tomentosa* are excluded from the lichen checklist of Papua New Guinea. All lichenicolous fungi observed on *Peltigera* thalli in Papua New Guinea are listed.

Key words: lectotypification, lichenicolous fungi, The Philippines, Indonesia, Irian Jaya, systematics, ITS

Article Information

Received 16 September 2008

Accepted 16 February 2009

Published online 1 October 2009

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Introduction

The genus *Peltigera* Willd. (Peltigera-ceae, lichenized Ascomycetes) is well represented in the mountains of Papua New Guinea, where it grows on soil, gravel, mossy rocks and tree trunks and branches. In his Catalogue of the lichens of Papua New Guinea and Irian Jaya (Indonesia), Streimann (1986: 96-98) reports nine taxa for the genus *Peltigera*: *P. canina* (L.) Willd. (with the mention that 'some collections may belong to a new species'), *P. dolichorhiza* (Nyl.) Nyl., *P. erioderma* Vain., *P. horizontalis* (Huds.) Baumg. (with the mention that these reports are misidentifications for *P. erioderma*), *P. laciniata* (G. Merr. ex Riddle) Gyeln. (with the mention that 'some collections may belong to a new species'), *P. cf. malacea*

(Ach.) Funk (with the mention 'record doubtful'), *P. polydactyla* (Neck.) Hoffm. (with the mention 'record doubtful'), *P. spuria* (Ach.) DC. (a species now named *P. didactyla* (With.) J.R. Laundon) and *P. tomentosa* Vain. *Peltigera ulcerata* Müll. Arg. has been added to that list by Aptroot and Sipman (1991: 232). Based on preliminary results of the present study, Martínez *et al.* (2003) mentioned *P. cichoracea* Jatta and *P. oceanica* Gyeln. from Papua New Guinea and the Papuan Provinces, respectively.

The taxonomy of the genus in Papua New Guinea is poorly understood due mainly to the application of taxonomic concepts elaborated in other regions of the world. The genus *Peltigera* has been revised for much of the Northern Hemisphere (e.g. Vitikainen 1994;

Goward *et al.* 1995), and parts of the southern hemisphere (e.g. Galloway, 2000) but tropical taxa remain critically understudied. Swinscow and Krog (1988) offered a treatment of East African species and Vitikainen (1998) provided a nomenclatural synopsis and preliminary key for the Neotropics (Vitikainen, 1998). Few comprehensive treatments of Asian taxa have been proposed: Awasthi and Joshi (1982) for India, and Stenroos *et al.* (1994) and Xi-Ling (1986) for parts of China.

Numerous collections of *Peltigera* are available from Papua New Guinea, based on material collected mainly by T. Koponen (H) and H. Streimann (CANB), and three expeditions organized in the country during the last 20 years (A. Aptroot and H. Sipman in 1987; A. Aptroot, P. Diederich, E. Sérusiaux and H. Sipman in 1992; A. Aptroot, P. Lambley, E. Sérusiaux and H. Sipman in 1995). These collections form the basis of the present taxonomic account.

The genus *Peltigera* has a pioneer status in modern lichen taxonomy as molecular techniques were here first used to delimitate species within a lichen genus: Goffinet and Miadlikowska (1999) described the new *P. phyllidiosa* from S-E United States, using ITS sequences of rDNA to distinguish it from related species (*P. collina* and *P. neckeri*); Goward and Goffinet (2000) followed a similar approach for the new *P. chionophila*, a representative of the *P. aphthosa*-group; and Goffinet *et al.* (2003) produced a robust phylogeny of the *P. didactyla*-group through analysis of nrDNA sequences. Furthermore, 38 described species and 8 putative undescribed taxa were examined in great detail by Miadlikowska and Lutzoni (2000), using morphological and chemical characters and LSU rDNA sequences. Their phylogenetic analysis led to an infrageneric reorganization of the whole genus. Finally, Miadlikowska *et al.* (2003) examined patterns in morphological variation in the *P. canina*-complex against phylogenetic inferences in ITS and LSU rDNA sequence including phylogenetic signal extracted from regions of ambiguous alignment using INAASE, a method developed by Lutzoni *et al.* (2000).

The present study provides the first taxonomic account of *Peltigera* in Papua New

Guinea, based on a critical study of morphological and chemical characters. We further sequenced the ITS region (nrDNA) for all but one regional species and complemented these with sequences publically available to assess the monophyletic nature and phylogenetic affinities of the species from Papua New Guinea. All taxa were placed and discussed in the context of the currently accepted infrageneric classification of the genus.

The present study is a part of the continuing effort towards a better knowledge of the tremendous lichen biodiversity in tropical mountains in S-E Asia (Aptroot *et al.*, 2007, Bjerke and Sipman, 2007, Jørgensen, 2007). A representative set of the species of *Peltigera* will be deposited at Papua New Guinea National Herbarium in Lae.

Material and methods

This study is based on approximately 430 specimens, and integrates critical morphological, chemical and molecular characters with field observations by the first author on habitat and geographical distribution. Ascospores measurements are given for apothecia sections prepared in water and only for spores that escaped the asci following gentle pressure on such thin sections. For the descriptions and use of terminology, we follow Vitikainen (1994: 5-17). Thin-layer-chromatography (TLC) has been performed for all specimens studied, following Orange *et al.* (2001) and using solvents C and G; the main purpose of this chemical analysis was to provide further characters for species delimitation and thus no effort was made to identify and name accessory terpenoids.

For DNA extraction, lobes margins or apothecia were sampled from herbarium specimens of each species. DNA was extracted using modified CTAB extraction by Doyle and Doyle (1987) or the NucleoSpin®Plant kit from Macherey Nagel (Düren, Germany) following the manufacturer's protocol. The Internal Transcribed Spacer region (ITS1, 5.8S and ITS2) of the nrDNA repeat was targeted with the Polymerase Chain Reaction using either the primers ITS1F (CTTGGTCATTTAG AGGAASTAA; slightly modified from Gardes and Bruns 1993 by Piercy-Normore *et al.* 2006)

or ITS1 (5'TCCGTAGGTGAACCTGCGG3') with ITS4 (5'TCCTCCGCTTATTGATATG C3', White *et al.* 1990) directly, or via a nested approach whereby the region was targeted first using the primers BMBC-R (5'GTACACA CCGCCCGTTCG3') and LS4R (5'TCAAGC ACTCTTTGACTCTC3', Shaw 2000), with the product of this initial PCR serving as the template for a second PCR using primers ITSF or ITS1 and ITS4. The amplification reaction was performed in a 25 μ L volume containing 0.75 units of HotMaster Polymerase Taq (Eppendorf), 2.5 μ L of its buffer, 1 μ L of a 10 μ M solution of the primers, 2.5 mM of each dNTP solution, and 1 μ L of genomic DNA. PCR products were screened on 1% agarose gels stained with ethidium bromide, and purified using NucleoSpin®Extract II kit from Macherey Nagel (Düren, Germany) following the manufacturer's protocol. Sequencing products were purified using Sephadex G-50 (Amersham) gel filters, and separated by capillary electrophoresis using the ABI Prism™ 3100 Genetic Analyzer. Nucleotide sequences were edited using Sequencher 3.1 (Gene Codes Corporation), entered in PAUP*version 4.0b10 for Macintosh-PPC (Swofford, 2002), and manually aligned.

All newly obtained sequences were submitted to GenBank (see Table 1 for accession numbers). The beginning and end of the ITS1 and the ITS2 spacers were determined by comparison with sequences available from GenBank. We excluded the 3' end of the 18S gene, and the 5' end of the 26S gene from the analyses. Sequences for specimens from Papua New Guinea were complemented with representatives of allopatric taxa, for which ITS sequences were available from GenBank; their accession number is provided in the figures (Figs 1-2). *Peltigera tereziana* and *P. polydactyloides* were also targeted for their ITS sequence (Table 1), to test their affinities to species from Papua New Guinea.

Internal Transcribed Spacers could not be readily aligned across all taxa; in fact, two groups emerged from visual alignment. Therefore, preliminary phylogenetic inferences were derived from the 5.8S gene, aligned across all sequences and analyzed using maximum parsimony (MP) bootstrapping (Felsenstein, 1985) with a heuristic search

algorithm on 200 pseudoreplicates each analyzed 200 times by randomly adding sequences; a limit of 1,000 trees saved per pseudoreplicate was imposed. The lineages recovered corresponded to the groups recognized based on visual alignment of the spacer regions. Consequently, subsequent analyses were restricted to sequences belonging to one or the other group and inferences could then be made from variation in the sequences of both spacers.

All sequences were then assigned to either of the two taxon sets corresponding to the Sections *Peltigera* and *Polydactylon* + *Horizontales* (Miadlikowska and Lutzoni, 2000). Phylogenetic relationships within these groups were reconstructed using *P. retifoveata* (Sect. *Retifoveata*) and members of the *P. neckeri* group of Sect. *Horizontales* as outgroups, respectively. Regions of ambiguous alignment across sequences within each of these two groups were excluded from phylogenetic analyses. Separate unweighted maximum parsimony analyses for the Sections *Peltigera* and *Polydactylon* + *Horizontales* were performed as follows in PAUP*4.0b10: an initial run performed by using the "tree bisection reconnection" (TBR) branch swapping algorithm, with the «steepest descent» option turned on, and only 10 trees saved for each of the 200 random addition replicates, was followed by a second analysis whereby all saved trees were swapped to completion with no limit to the number of trees saved. All other parameters were set to the default options (e.g., gaps were treated as missing data). Support for the branches was estimated using the bootstrap approach with a heuristic search algorithm on 300 pseudoreplicates each analyzed 2 times by randomly adding sequences; a limit of 1000 trees saved per pseudoreplicate was imposed. Bootstrap frequencies (MPBS) were obtained by constructing a majority rule consensus tree of all trees saved during the analysis.

For the second set of the MP analyses, symmetric step matrices were created for unambiguous portions of the alignments using the STMatrix 2.1 (Francois Lutzoni and Stefan Zoller, Department of Biology, Duke University), as outlined in Miadlikowska *et al.* (2003). ITS1, ITS2 and 5.8S each were subjected to a specific symmetric step matrix. Gaps from the

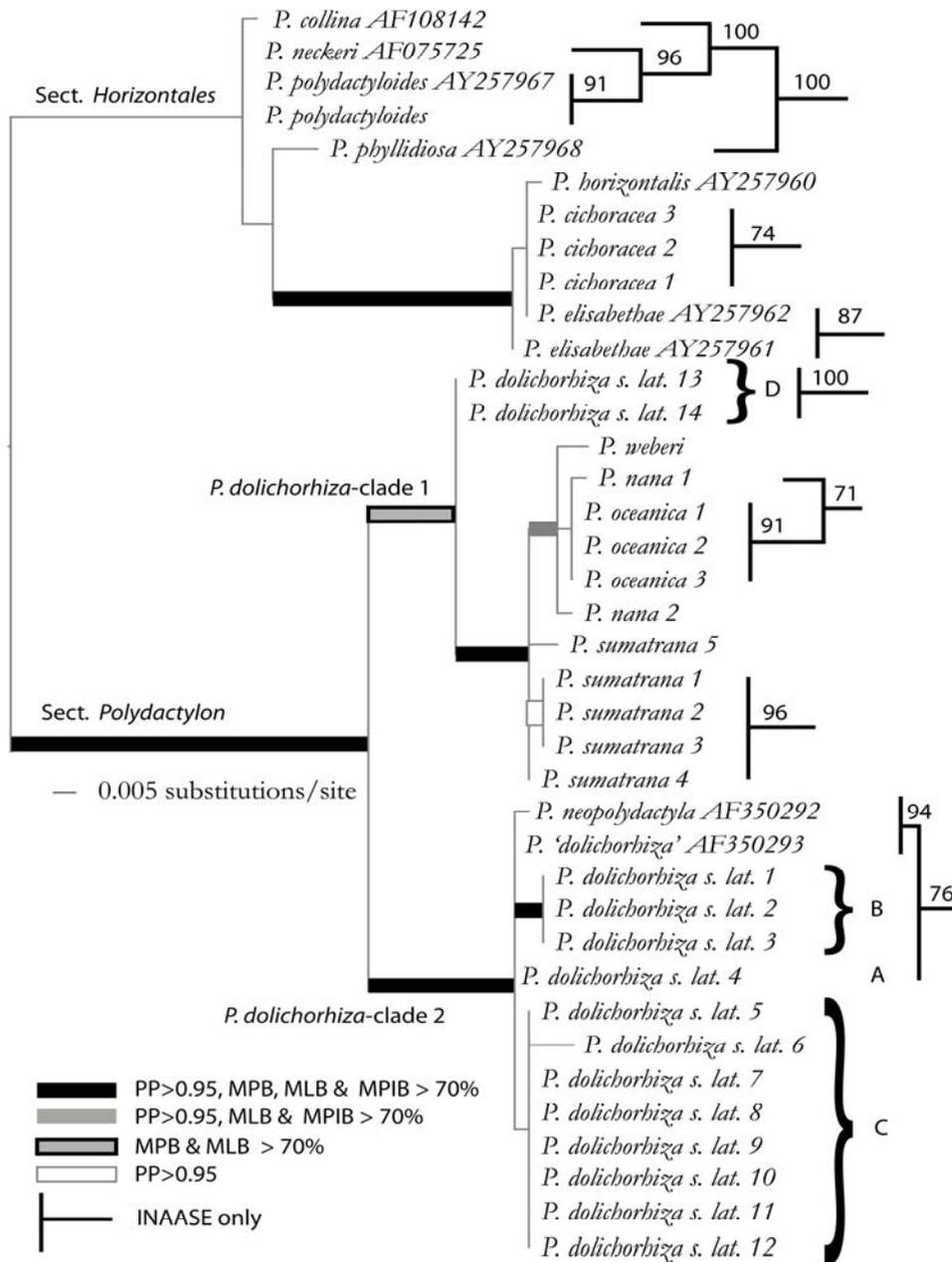


Fig. 1. Phylogenetic relationships of species of the *Peltigera polydactylon* s. lat.-clade (i.e., *Peltigera* Sect. *Horizontales* and *Polydactylon* sensu Miadlikowska and Lutzoni 2000) occurring in Papua New Guinea, inferred from ITS sequences. Single most likely tree ($-\ln = 926.58436$). Alternative relationships supported via MP+INAASE analyses are shown to the right. Support is indicated for branches characterized by posterior probabilities > 0.95 , or bootstrap frequencies exceeding 70% under maximum parsimony (MPB) or maximum likelihood (MLB). Bootstrap support derived from the MP+INAASE (MPIB) is specified for branches not present in the most-likely tree.

unambiguous portions of the alignments were treated as a fifth character state. Phylogenetic signal from ambiguously aligned portions of the alignments was integrated into maximum parsimony analyses without violating positional homology, using the program INAASE 2.3b (Lutzoni *et al.*, 2000), a method now currently used in phylogenetic studies of lichenized fungi (Amtoft *et al.*, 2008, Gaya *et al.*, 2008, Reeb *et al.* 2007). All substitutions were equally weighted (1.0). In addition, the

hypervariable region within the ITS1 (ITS1-HR; Miadlikowska *et al.*, 2003) for the Sect. *Peltigera* was recoded into 23 characters using the program arc v1.5 (Kauff *et al.*, 2003; Miadlikowska *et al.*, 2003) with the nucleotide option, as outlined in Reeb *et al.* (2004). Each of the 23 characters obtained with arc-nucleotide were subjected to a specific weight: 1.00 for character 1; 0.25 for characters 2–5; 0.10 for characters 6–15 and 0.50 for characters 16–23. Weighted MP analyses with recoded

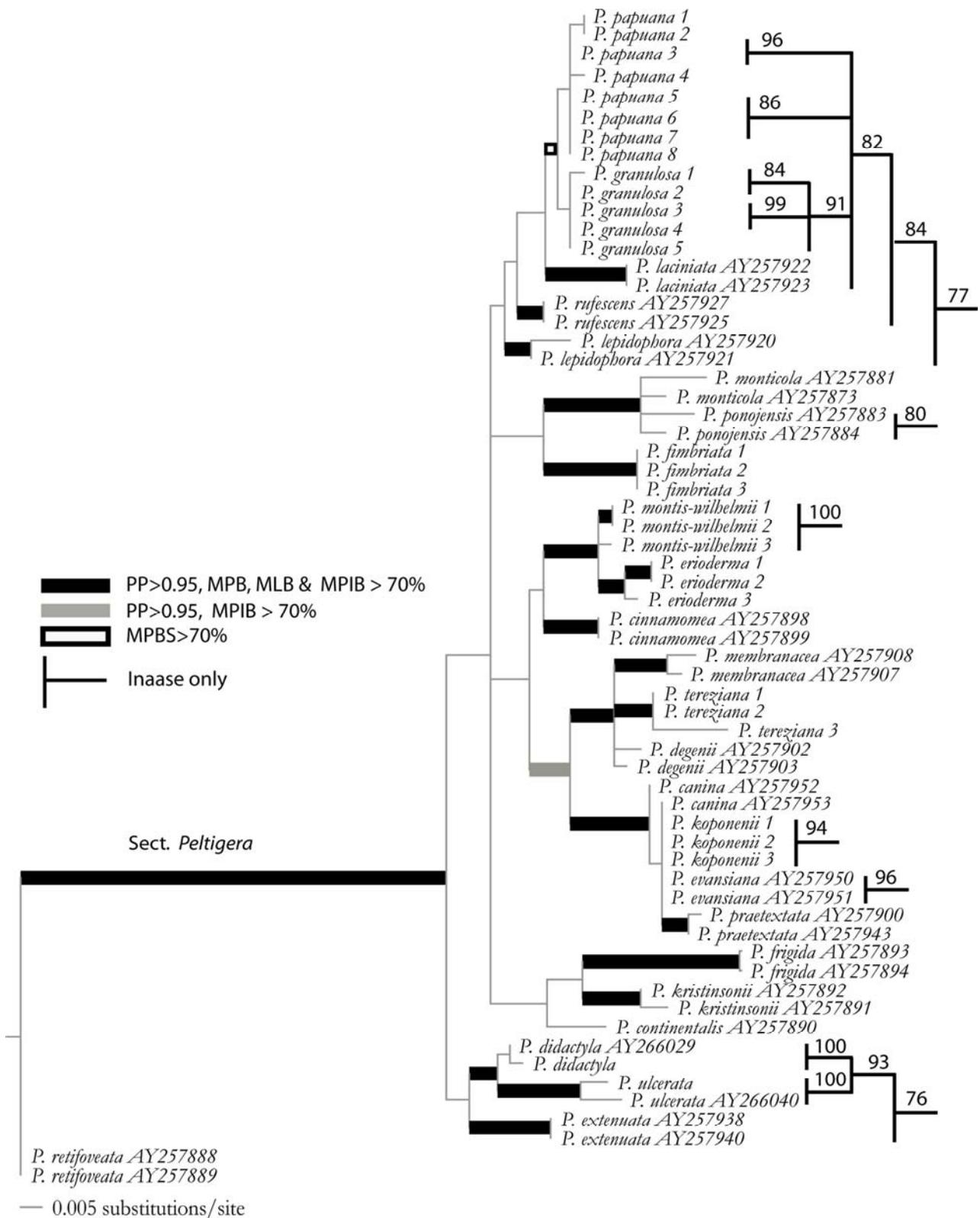


Fig. 2. Phylogenetic relationships of species of the *Peltigera canina*-clade (i.e., *Peltigera* Sect. *Peltigera* sensu Miadlikowska and Lutzoni, 2000) occurring in Papua New Guinea inferred from ITS sequences. Single most likely tree ($-\ln = 1538.2922$). Alternative relationships supported via MP+INAASE analyses are shown to the right. Support is indicated for branches characterized by posterior probabilities > 0.95, or bootstrap frequencies exceeding 70% under maximum parsimony (MPB) or maximum likelihood (MLB). Bootstrap support derived from the MP+ INAASE (MPIB) is specified for branches not present in the most-likely tree.

Table 1. Voucher information for specimens of *Peltigera* for which the ITS region was sequenced. Sequences are identified by their GenBank accession numbers. All vouchers from Papua New Guinea and deposited in LG unless otherwise indicated.

Taxon	Voucher	GenBank
<i>P. cichoracea</i> 1	Huon peninsula, July 1992, <i>E. Sérusiaux</i> s. n.	FJ527278
<i>P. cichoracea</i> 2	Myola, <i>E. Sérusiaux</i> 15305	FJ527277
<i>P. cichoracea</i> 3	Mt Wilhelm, <i>E. Sérusiaux</i> 13983	FJ527276
<i>P. didactyla</i>	Mt Sarawaket, <i>T. Koponen</i> 32182	FJ527258
<i>P. dolichorhiza</i> s. lat. 1	Myola, <i>H. Sipman</i> 38337 (B)	FJ527295
<i>P. dolichorhiza</i> s. lat. 2	Myola, October 1995, <i>E. Sérusiaux</i> s. n. (sample 1)	FJ527301
<i>P. dolichorhiza</i> s. lat. 3	Myola, October 1995, <i>E. Sérusiaux</i> s. n. (sample 2)	FJ527302
<i>P. dolichorhiza</i> s. lat. 4	Bundi gap, <i>P. Diederich</i> 11052 (hb Diederich)	FJ527294
<i>P. dolichorhiza</i> s. lat. 5	Myola, October 1995, <i>E. Sérusiaux</i> s. n. (sample 3)	FJ527292
<i>P. dolichorhiza</i> s. lat. 6	Gahavisuka, <i>P. Diederich</i> 10582 (hb Diederich)	FJ527293
<i>P. dolichorhiza</i> s. lat. 7	Teptep, <i>T. Koponen</i> 34738 (H)	FJ527296
<i>P. dolichorhiza</i> s. lat. 8	Teptep, 30 July 1992, <i>E. Sérusiaux</i> s. n.	FJ527297
<i>P. dolichorhiza</i> s. lat. 9	Teptep, <i>T. Koponen</i> 34691 (H)	FJ527298
<i>P. dolichorhiza</i> s. lat. 10	Gahavisuka, 5 November 1995, <i>E. Sérusiaux</i> s. n.	FJ527299
<i>P. dolichorhiza</i> s. lat. 11	Myola, <i>H. Sipman</i> 38261 (B)	FJ527300
<i>P. dolichorhiza</i> s. lat. 12	Gahavisuka, <i>H. Sipman</i> 22199 (B)	FJ527303
<i>P. dolichorhiza</i> s. lat. 13	Myola, October 1995, <i>E. Sérusiaux</i> s. n. (sample 4)	FJ527279
<i>P. dolichorhiza</i> s. lat. 14	Saruwaged Range, <i>H. Sipman</i> 24434 (B)	FJ527280
<i>P. erioderma</i> 1	Myola, October 1995, <i>E. Sérusiaux</i> s. n. (sample 1)	FJ527263
<i>P. erioderma</i> 2	Myola, October 1995, <i>E. Sérusiaux</i> s. n. (sample 2)	FJ527264
<i>P. erioderma</i> 3	Mt Wilhelm area, <i>E. Sérusiaux</i> 14107	FJ527265
<i>P. fimbriata</i> 1	Mt Sarawaket, <i>T. Koponen</i> 32996 (isotype)	FJ527272
<i>P. fimbriata</i> 2	Teptep, <i>T. Koponen</i> 33912 (H)	FJ527273
<i>P. fimbriata</i> 3	Mt Wilhelm, <i>A. Aptroot</i> 33080 (hb Aptroot)	FJ527274
<i>P. granulosa</i> 1	Bundi, November 1995, <i>E. Sérusiaux</i> s. n. (sample 1)	FJ527253
<i>P. granulosa</i> 2	NE of Mt Sarawaket, <i>T. Koponen</i> 33267 (isotype)	FJ527254
<i>P. granulosa</i> 3	Myola, <i>E. Sérusiaux</i> 15150	FJ527255
<i>P. granulosa</i> 4	Bundi, <i>H. Sipman</i> 39313 (B)	FJ527256
<i>P. granulosa</i> 5	Bundi, November 1995, <i>E. Sérusiaux</i> s. n. (sample 2)	FJ527257
<i>P. koponenii</i> 1	Lake Wamba, <i>T. Koponen</i> 34327 (isotype)	FJ527269
<i>P. koponenii</i> 2	Myola, October 1995, <i>E. Sérusiaux</i> s. n.	FJ527270
<i>P. koponenii</i> 3	Oksapmin, <i>L. Hoffman</i> 90-103	FJ527271
<i>P. montis-wilhelmii</i> 1	Mt Wilhelm, <i>E. Sérusiaux</i> 13984 (holotype)	FJ527260
<i>P. montis-wilhelmii</i> 2	Mt Wilhelm, <i>D. McVean</i> 66236 (COLO)	FJ527261
<i>P. montis-wilhelmii</i> 3	Goroka-Gembolg, August 1992, <i>E. Sérusiaux</i> s. n.	FJ527262
<i>P. nana</i> 1	Bundi, November 1995, <i>E. Sérusiaux</i> s. n.	FJ527282
<i>P. nana</i> 2	Mt Wilhelm, <i>E. Sérusiaux</i> 13981	FJ527286
<i>P. oceanica</i> 1	Myola, October 1995, <i>E. Sérusiaux</i> s. n.	FJ527283
<i>P. oceanica</i> 2	Onim Station, <i>A. Bellamy</i> 1295 (B)	FJ527284
<i>P. oceanica</i> 3	Mt Sarawaket, <i>T. Koponen</i> 31965	FJ527285
<i>P. papuana</i> 1	Teptep, <i>E. Sérusiaux</i> 13656 (holotype)	FJ527246
<i>P. papuana</i> 2	Mt Wilhelm area, <i>E. Sérusiaux</i> 14106	FJ527247
<i>P. papuana</i> 3	Mt Sarawaket, <i>T. Koponen</i> 31592 (H)	FJ527245
<i>P. papuana</i> 4	Mt Gahavisuka, <i>P. Diederich</i> 10581 (hb. Diederich)	FJ527249
<i>P. papuana</i> 5	Myola, <i>H. Sipman</i> 38336 (B) (sample 1)	FJ527248
<i>P. papuana</i> 6	Teptep, <i>E. Sérusiaux</i> 13655	FJ527252
<i>P. papuana</i> 7	Myola, <i>H. Sipman</i> 38336 (B) (sample 2)	FJ527251
<i>P. papuana</i> 8	Teptep, <i>H. Sipman</i> 35270 (B)	FJ527250
<i>P. polydactyloides</i>	KENYA, Mt Kenya, September 2002, <i>D. Killmann</i> (KOBL)	FJ527275
<i>P. sumatrana</i> 1	Gahavisuka, <i>P. Diederich</i> 10585 (hb Diederich)	FJ527288
<i>P. sumatrana</i> 2	Mt Wilhelm, <i>E. Sérusiaux</i> 13985	FJ527289
<i>P. sumatrana</i> 3	Gahavisuka, November 1995, <i>E. Sérusiaux</i> s. n.	FJ527290
<i>P. sumatrana</i> 4	Bundi, <i>E. Sérusiaux</i> 16402	FJ527291
<i>P. sumatrana</i> 5	Saruwaged Range, <i>H. Sipman</i> 24513 (B)	FJ527287
<i>P. tereziana</i> 1	AUSTRALIA, NSW, <i>T. K. Overeem</i> 11 (CANB)	FJ527266

Table 1 (continued). Voucher information for specimens of *Peltigera* for which the ITS region was sequenced. Sequences are identified by their GenBank accession numbers. All vouchers from Papua New Guinea and deposited in LG unless otherwise indicated.

Taxon	Voucher	GenBank
<i>P. tereziانا</i> 2	AUSTRALIA, NSW, <i>J. A. Elix</i> 24690 (CANB)	FJ527267
<i>P. tereziانا</i> 3	AUSTRALIA, NSW, <i>H. Streimann</i> 63484 (CANB)	FJ527268
<i>P. ulcerata</i>	Gahavisuka, <i>E. Sérusiaux</i> 16200	FJ527259
<i>P. weberi</i>	Bundi, <i>H. Sipman</i> 39314 (B)	FJ527281

INAASE characters (for the Sect. *Peltigera* and *Polydactylon+Horizontales*) and arc characters (for the Sect. *Peltigera* only) were performed as heuristic searches with 1000 random-addition-sequence replicates, TBR branch swapping, MulTrees option in effect, saving all trees and collapsing branches with maximum branch length equal to zero. Hereafter, these weighted MP analyses will be referred to as MP+INAASE. Branch support was assessed by MP bootstrap analyses with full heuristic searches, 1000 replicates using two random addition sequence (RAS) per bootstrap replicate and by saving all trees. In both bootstrap analyses, the same parameters as in the original MP search were used, and constant sites were excluded from all the analyses.

The optimal model of sequence evolution for each matrix was identified using MrModeltest 2 (Nylander, 2004) based on the Akaike Information Criterion (Posada and Buckley 2004). The model that was selected for the Sections *Polydactylon+Horizontales* corresponds to the K80 (Kimura, 1980) + I model, which was implemented as follows: transition/transversion ratio = 2.0140; base frequencies are equal; proportion of invariable sites = 0.5875. The model that was selected for the Sect. *Peltigera* corresponds to the SYM (Zharkikh, 1994) + G model. The substitution rates were fixed to: 1.1668 (A-C), 4.5587 (A-G), 1.6528 (A-T), 0.2951 (C-G) and 4.5772 (C-T); the proportion of invariable sites was set to zero and the gamma distribution shape parameter to 0.2939. Maximum likelihood (ML) search was performed using PAUP*4.0b10, invoking the «steepest descent» option and using the «TBR branch swapping» algorithm. The search strategy implemented for the bootstrap search was the same as that used in unweighted MP: 300 pseudoreplicates, each with two random additional replicates, TBR

and a maximum of 1000 trees saved per replicate. Trees saved during the bootstrap search were executed in PAUP and a 70% majority-rule consensus tree built. Bootstrap frequencies were considered significant if higher than 70% (Hillis and Bull, 1993; Reeb *et al.*, 2004). Likelihood trees were sampled from the tree space using a Bayesian approach (MrBayes v.3.1.2; Ronquist and Huelsenbeck, 2003) using three heated and one cold chains. The data were treated as a single partition. A single tree was saved to a tree file every 50 generations for a total of 10^6 generations. Of the 20,001 trees that were saved, the first 1001 (the “burnin”) were ignored for determining posterior probabilities and confidence intervals for model parameters. The Bayesian analyses were repeated once to allow for the presence of multiple local optima. The trees that were sampled during both runs were ultimately combined and parameter and posteriors were estimated based on this set of 36,000 trees. Posterior probabilities (PP) for bipartitions, drawn from the 95% consensus tree were considered statistically significant when the $P \geq 0.95$.

Both final datasets for the *P. polydactylon* s. lat.-group and the *P. canina*-group are deposited in TreeBASE.

Results

Phylogenetic analysis of the ITS sequences

The ITS region was successfully sequenced for 60 specimens including three accessions of the Australasian *P. tereziانا* and one accession of the African *P. polydactyloides* (Table 1). DNA suitable for the amplification of the ITS region could not be obtained for Papua New Guinea samples of *P. extenuata*, additional samples of *P. erioderma*, *P. fimbriata*, *P. ulcerata*, and *P. weberi*. Incomplete

sequences were obtained for *P. cichoracea* 3 and *P. sumatrana* 1 (each missing about 150 nucleotides [nts] in the ITS1), and *P. dolichorhiza* s. lat. 5, for which the ITS1 is missing the first 12 nts. For all three accessions of *P. fimbriata* only the 5.8S and the ITS2 region could be sequenced.

Alignment of the sequences led to multiple regions of ambiguous homology. An analysis of the 5.8S gene segregated the sequences into two groups, corresponding to Sect. *Peltigera* (hereafter named the *P. canina*-clade) and Sect. *Horizontales*+*Polydactylon* (hereafter named the *P. polydactylon* s. lat.-clade), respectively. Within these two clades the spacer sequences aligned more readily (although large regions of ambiguous alignment remained), and consequently analyses were conducted on these groups separately.

Overall, sequence variation within the ITS region permits to circumscribe the Sections of *Peltigera* and various species complexes within them, but fails to provide strong evidence for the monophyly of various species that seem well-defined on morphological and chemical grounds. The ITS regions are characterized by significant local length variations. The pattern is often congruent with species delimitations and this putative phylogenetic signal is indeed recovered when integrating these regions in maximum parsimony analysis as coded characters. *Peltigera fimbriata* and *P. montis-wilhelmii* are well-defined by the ITS1-HR region, which is unique for each putative species. High intraspecific variation in the ITS1-HR region within *P. papuana* may indicate presence of multiple unrecognized species. For example, *P. papuana* 2 & 3 share an almost identical ITS1-HR pattern that differs from the remaining specimens of *P. papuana*. In the case of *P. koponenii* the pattern in the ITS1-HR region is identical to that observed in *P. canina* specimens included in this study, but the species is defined by two single nucleotide changes (one substitution and one guanosine insertion). Phylogenetic signal recovered from ambiguous regions of the alignment thus generally permits to enhance resolution within species complexes, and never significantly contradicts phylogenetic relationships derived from the alignable portions of the spacers, as already shown in previous phyloge-

netic reconstructions within *Peltigera* (Miadlikowska *et al.*, 2003; Goffinet *et al.*, 2003) or other genera (*Pseudocyphellaria*: Miadlikowska *et al.*, 2002; *Teloschistaceae*: Gaya *et al.*, 2003, 2008; *Sticta*: McDonald *et al.*, 2003; polyporous genera: Reeb *et al.*, 2004).

Several morphologically well-defined taxa failed to be resolved as monophyletic entities based on ITS. Examples include *P. evansiana*, an Eastern North American-Eastern Asian taxon diagnosed from all its congeners by the small granular laminal isidia or *P. elisabethae*, a circumboreal species differing from its closest relatives by the schizidia. With regard to the Papua New Guinea *Peltigera*, several morphotaxa lack support for their monophyly, such as *P. koponenii*, *P. montis-wilhelmii*, or *P. granulosa*. However, inferences from ITS fail to provide strong support against the hypothesis of monophyly for these taxa. This lack of a robust resolution despite morphological differentiation may merely reveal broad morphological amplitude or be indicative of recent or active speciation events. Recent cladogenic events can only be recovered within a phylogenetic scenario through the extensive sampling of fast evolving loci (Knowles and Carstens, 2007). At present such loci have not yet been identified for *Peltigera*, and ITS remains a main source of information to address the phylogenetic significance of morphological and chemical characters in this genus.

***The Peltigera polydactylon* s. lat. clade** (Fig. 1)

Within this clade, the ITS1 varied between 185 in *P. phyllidiosa* and 237 nts in *P. dolichorhiza* s. lat. 5, 6, 9, 10 & 11. The alignment of the sequences resulted in a matrix of 757 characters of which 439 ambiguously aligned characters were excluded from heuristic searches for unweighted MP and ML analyses. Of the 318 characters included in the analyses, 248 were constant, and 59 potentially informative under the parsimony criterion. Twenty-two regions of ambiguous alignment were recoded using INAASE and included in the weighted MP analyses.

The heuristic search based on the nucleotide characters only yielded a set of six equally parsimonious trees of length 89 (CI = 0.9101, CI-auto = 0.8947; RI = 0.9865, RC =

0.8978; trees not shown). Inferences under ML using PAUP converged on a single tree (-ln=926.58436) that is topologically congruent with those obtained under MP. The monophyly of Sect. *Polydactylon* and that of its two main clades is well supported. Extracting phylogenetic signal from regions of ambiguous alignment (INAASE characters) provided more resolution and support for many morphospecies and phylogenetic relationships among them.

Peltigera cichoracea is placed within the *P. horizontalis* group (MPBS=100%; MPIBS=95%; MLBS=100%; PP=1.00). Differentiation of the species based on ITS data is weak, consisting primarily in short, mostly single nucleotide indels. The monophyly of *P. cichoracea* and of *P. elisabethae* is confirmed when INAASE characters were included in the MP analysis (MIPBS=74% and 87%, respectively).

Within the well-supported Sect. *Polydactylon*, two main lineages are resolved. The first clade (hereafter named Clade 1) is composed of *P. nana*, *P. oceanica*, *P. sumatrana* and *P. weberi*, and two specimens referred to *P. dolichorhiza* s. lat. D. Validity of all sequences from Clade 1 have been confirmed via new extractions, amplifications and sequencing. This combined lineage is well supported in terms of bootstrap percentages (MPBS=84%; MLBS=88%) but fails to gather strong support from the Bayesian (PP=0.92%) and MP+INAASE analyses (MPIBS=52%). The two *P. dolichorhiza* specimens share identical sequences except of a dinucleotide duplication in the ITS1 of *P. dolichorhiza* 13. They share only indels as synapomorphies and hence they form a well-supported monophyletic clade only when indels are scored 1.00 (MPIBS=100%). None of the analyses revealed *P. sumatrana* as monophyletic. The five accessions share few if any synapomorphies, unlike their relatives. The monophyly of the clade combining *P. nana*, *P. oceanica*, and *P. weberi* is well supported (MPIBS=98%; MLBS=78%; PP=0.99) except under unweighted MP when indels are not scored (MPBS=66%). Within this group, only *P. oceanica* is represented by several specimens collected in different localities. Monophyly of *P. oceanica* is well supported in the MP+INAASE analysis (MPIBS=91%). The relationships among *P. nana*, *P. oceanica*, *P. sumatrana* and *P. weberi* are ambiguous. The

phylogenetic structure is congruent with patterns of indel distribution: the clade 1 is defined among others by lacking a 25 nts long region in the ITS2; *P. sumatrana* differs from its relatives by a single versus a double TAA repeat, a GATA insertion and an 11 nts deletion in the ITS2 compared to other members of the clade.

The second clade (MPBS=98%; MLBS=94%; MPIBS=100%; PP=1.00) comprises mainly specimens that are morphologically identified as *P. dolichorhiza* and two GenBank accessions filed as *P. dolichorhiza* and the bipolar *P. neopolydactyla* (both specimens were collected in New Zealand; Thomas *et al.*, 2002). This clade is hereafter referred to as Clade 2. The sequences within this group are identical except for a three nucleotide duplication in the ITS1 shared by five accessions, and an additional T in a poly-T region in the ITS2. The pattern of sequence variation among the specimens from Papua New Guinea included in Clade 2 matches that of the chemical variation. Indeed, three chemotypes are recognized: one is characterized by the production of peltidactylin and zeorin and is represented by a single accession (*P. dolichorhiza* s. lat. 4); the second one is represented by eight accessions (*P. dolichorhiza* s. lat. 5-12), all with the unique chemical pattern of four unknown terpenes together with methyl gyrophorate, tenuiorin, methyl lecanorate, methyl evernate, and methyl orsellinate; the third group of three specimens (*P. dolichorhiza* s. lat. 1-3) represents samples from the same locality and is characterized by the production of zeorin, and rather short, fasciculate or densely branched rhizines (vs long and simple for the other accessions of Clade 2).

It is worth mentioning that both clades are morphologically variable but that differentiation between them is lacking. The only diagnostic character seems to be the presence or absence of dolichorrhizin: abundantly produced in Clade 1, and never (or not clearly detected) in Clade 2. However, this diagnostic character vanishes when sequences from specimens from Rwanda (Africa) morphologically identified as *P. dolichorhiza* are included (Goffinet and Sérusiaux, unpubl. results): they produce dolichorrhizin but unambiguously fall within Clade 2.

The importance of chemistry within the Sect. *Polydactylon* was first detected by Miadlikowska and Lutzoni (2000), who even provided a key to the chemotypes present. They described a pattern (Fig. 10 in Miadlikowska and Lutzoni, 2000: 947) which is present in the material from Papua New Guinea: a chemotype with the three main terpenes present (peltidactylin, dolichorrhizin and zeorin) and others with one or two missing. A similar variation was earlier described by Holtan-Hartwig (1993: 58) for *P. neopolydactyla*: two chemotypes with the three main terpenes present (the chemotypes being differentiated by the occurrence of secondary ones), a chemotype without dolichorrhizin and one with zeorin only. Furthermore chemotypes were correlated with morphological variation, including the morphotype C with «thick, bush-shaped to slightly branched rhizines» associated with the chemotype producing only zeorin (plus a secondary one). Interestingly, *P. dolichorhiza* s. lat. 1-3 could match such a description.

The delimitation between *P. neopolydactyla* and *P. dolichorhiza* remains ambiguous. *Peltigera dolichorhiza* is traditionally considered to be restricted to the southern Hemisphere with some extension into subtropical areas North of the Equator (Ahti and Vitikainen, 1977: 93), and has on that basis been excluded from temperate and boreal floras (ex.: Goffinet and Hastings, 1994: 36-37). *Peltigera neopolydactyla* is by contrast thought to be primarily (but not exclusively) circumboreal in distribution. Where the species are sympatric they are distinguished on subtle tinge differences of both sides of the thallus (Neotropics: Vitikainen, 1998) or on the size and branching of the rhizines (New Zealand: Galloway, 2000). *Peltigera neopolydactyla* has been extensively studied in Europe and Canada, where it is morphologically and chemically variable (Holtan-Hartwig, 1993: 57-62; Vitikainen, 1994: 67-69; Goward *et al.*, 1995: 107-108).

The ITS was sequenced for both species by Thomas *et al.* (2002), on material from New Zealand and both samples are resolved within the clade 2. We have not examined the vouchers and it is possible that both are in fact *P. neopolydactyla* or that they represent a distinct taxon. Similarly, the whole Clade 2

could be interpreted as representing *P. neopolydactyla* or one or more distinct taxa. At present this ambiguity cannot be resolved. This putative complex of broadly lobed glabrous *Peltigera* species is in need of a critical taxonomic and phylogenetic revision. Pending further research on Clades 1 and 2, we do not give any status to the four chemotypes recognized as *P. dolichorhiza*.

The Peltigera canina clade (Fig. 2)

Within this group, the ITS1 varied between 162 in *P. rufescens* and 290 nts in *P. membranacea*. For *P. montis-wilhelmii* 2 the sequence is incomplete, and lacks about 20 nts at the 3' end. The alignment of the sequences that vary in length between 506 and 646 resulted in a matrix of 768 characters. Of these 337 were included in the analysis. Of these, 236 are constant, and 82 are potentially phylogenetically informative under parsimony. The largest portion of excluded characters belongs to the ITS1, and is composed primarily of the hypervariable region *sensu* Miadlikowska *et al.* (2003). Fifteen regions of ambiguous alignment were recoded using INAASE and included in the weighted MP analyses together with 23 are characters derived from the ITS1-HR region.

The heuristic search under maximum parsimony with nucleotide characters only yielded 30 optimal trees of 184 steps (CI = 0.6793, CI-auto = 0.6424; RI = 0.8865, RC = 0.6023). The nodes of the backbone are characterized by low support, and the phylogenetic signal carried by the aligned portions of the sequences is confined to the monophyly of individual species or closely related species. Analyses under the criterion of maximum likelihood yielded a single tree (-ln = 1538.2922). Bootstrap support (i.e. frequencies >70%) under maximum likelihood is congruent with maximum parsimony support. Posterior probabilities equal or greater than 0.95 are also confined to the monophyly of species or of closely related taxa (i.e. *P. canina* s. lat.). The addition of recoded characters (INAASE + arc) provided additional bootstrap support for species or species complexes such as *P. granulosa*, *P. koponenii*, *P. montis-wilhelmii*. The only taxon for which the support was always lacking is *P. papuana*.

Peltigera erioderma (MPBS=83%; MPIBS=93%; MLBS=80%; PP=1.00) is the sister-group to a clade composed of three accessions assigned to the newly described *P. montis-wilhelmii* (MPIBS=86%). These two taxa differ in their signature sequence in one variable region, with *P. montis-wilhelmii* exhibiting slight infraspecific variability. The shared most recent common ancestry is well supported (MPBS=97%; MPIBS=100%; MLBS=95%; PP=1.00), as well as by two unique insertions (2 and 1 nt) in the 5.8S gene. The *P. canina*-complex comprises another set of specimens from Papua New Guinea, representing the morphologically distinct *P. kopenhagenii*, represented by sequences virtually identical to those of *P. canina* (including the ITS1-HR region) except for one substitution and one single nucleotide insertion in unambiguous portion of the alignment. *Peltigera kopenhagenii* was reconstructed as monophyletic and highly supported (MPIBS=94%) when phylogenetic signal from ambiguous regions was incorporated into phylogenetic analyses (MP with recoded INAASE and arc characters).

The three accessions of *P. fimbriata* form a well-supported monophyletic group that may be closely related to the common ancestor to *P. ponojensis* and *P. monticola*, but such affinity remains ambiguous.

The remaining accessions from Papua New Guinea belong to a clade related to the cosmopolitan *P. rufescens*. The monophyly of *P. granulosa* is well supported only by MP with recoded INAASE and arc characters (MPIBS=91%). The monophyly of *P. papuana* lacks support.

Peltigera tereziana from Australia represents a well-supported monophyletic group, closely related to *P. degenii* and *P. membranacea*, but of ambiguous affinities to either one of these.

Key to species

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| <p>1a Soredia or soredioid masses present, at least in parts of the thalli 2</p> <p>1b Soredia or soredioid masses absent 7</p> <p>2a Upper surface tomentose, at least in parts; soralia mostly laminal, or submarginal on old thalli 3</p> | <p>2b Upper surface glabrous; soralia laminal, submarginal or marginal 4</p> <p>3a Rhizines abundant, densely branched to fibrillose; young soralia C+ red <i>P. extenuata</i></p> <p>3b Rhizines sparse, simple to loosely branched; soralia C- <i>P. didactyla</i></p> <p>4a Genuine soralia only 5</p> <p>4b Genuine soralia present but always with soredioid or isidioid masses, or with granules or phyllidia ... 6</p> <p>5a Soralia mostly laminal, or submarginal and marginal; terpenoids absent <i>P. ulcerata</i></p> <p>5b Soralia strictly marginal; terpenoids present <i>P. weberi</i></p> <p>6a Margins disrupted into soralia, soredioid or isidioid masses, or with granules or phyllidia; terpenoids present with zeorin always abundantly produced; thalli usually quite large, reaching 10 cm in diam. ... <i>P. cichoracea</i></p> <p>6b Margins with soralia or isidioid masses, when well-developed also present on the edge of the lower surface; terpenoids absent; thalli usually quite small, not exceeding 2-5 cm in diam. <i>P. granulosa</i></p> <p>7a Marginal lobules or phyllidia present 8</p> <p>7b Marginal lobules or phyllidia absent 9</p> <p>8a Upper surface smooth or faintly to distinctly scabrous, sometimes with a whitish pruina near the lobes margins resulting in a frosted appearance, lobes carrying the apothecia usually tomentose; marginal phyllidia usually abundant, but sometimes few; lower surface with a conspicuous network of usually dark, raised veins; rhizines mostly threadlike or penicillate; apothecia typically horizontal; terpenoids absent <i>P. papuana</i></p> <p>8b Upper surface smooth, rarely with a whitish pruina on lobes margins; marginal phyllidia rare (on lateral lobes or on damaged parts); lower surface usually lacking distinct veins; rhizines typically fasciculate and densely branched, remaining isolate and arranged in concentric rows or forming dense cushions under the thallus; apothecia typically saddle-shaped; terpenoids present <i>P. sumatrana</i> (rare forms)</p> <p>9a Upper surface tomentose, at least in parts; terpenoids absent 10</p> <p>9b Upper surface glabrous or pruinose (in parts or at the extremities of young lobes); terpenoids present or absent 14</p> <p>10a Rhizines usually very abundant and forming dense 'bushy' masses, typically fibrillose to coralloid; apothecia saddle-shaped <i>P. kopenhagenii</i></p> <p>10b Rhizines abundant or not, simple, threadlike, penicillate or fasciculate, never fibrillose to coralloid; apothecia horizontal or saddle-shaped 11</p> |
|--|--|

- 11a Apothecia typically horizontal; pycnidia absent, or rare and inconspicuous; tomentum covering large parts of the thallus, or restricted to lobes carrying the apothecia..... 12
- 11b Apothecia typically saddle-shaped; pycnidia usually present, at least on some lobes margins, conspicuous (0.3-0.8 mm in diam.); tomentum of the upper surface most usually well-developed, but sometimes absent in parts of the thallus, with long and conspicuous (to 1-1.4 mm long) hairs or not.... 13
- 12a Thallus large, to 15 cm in diam., lobes typically rounded at their extremities and 1-1.5 cm wide, margin revolute; tomentum present on most of the upper surface made of tiny whitish hairs (0.1-0.15 mm high) out of which longer ones (0.1-0.4 mm long) may emerge..... *P. erioderma*
- 12b Thallus forming attractive, small rounded rosettes (3-6 cm in diam. in suitable conditions); lobes imbricate, not exceeding 0.5-0.7 cm wide, with raised and crenate (sometimes +/- crisped) margins; tomentum usually restricted to lobes carrying apothecia but sometimes covering large parts of the thallus surface..... *P. papuana* (rare forms)
- 13a Tomentum of the upper surface sometimes almost absent in parts of the thallus but always, and especially near the lobes margins, with long (1-1.4 mm long) whitish to brownish hairs, sometimes aggregated in tufts; lobes rounded; rhizines not typically arranged in rows on the veins of young lobes *P. fimbriata* (typical populations)
- 13b Tomentum of the upper surface identical but with shorter hairs, sometimes quite few and hardly distinct from the tomentum, or even absent; lobes rather elongated and narrow; rhizines typically arranged in rows on the veins (especially on young lobes)..... *P. fimbriata* (atypical populations)
- 14a Apothecia typically horizontal; terpenoids absent... .. *P. montis-wilhelmii*
- 14b Apothecia saddle-shaped or absent; terpenoids present 15
- 15a Tenuiorin and methylglyrophosphate absent but terpenoids present; upper surface smooth, sometimes slightly pruinose at the margins or incrustated; lobes with raised and crisped lateral margins..... *P. oceanica*
- 15b Tenuiorin and methylglyrophosphate always produced, together with terpenoids 16
- 16a Rhizines abundant, or rarely sparse, rather short, fasciculate or densely branched..... 17
- 16b Rhizines sparse or abundant, most usually long and simple 19
- 17a Terpenoids present, mostly zeorin or peltidactylin but dolichorrhizin not produced *P. dolichorhiza* s. lat. **B**
- 17b Terpenoids present, dolichorrhizin abundantly produced..... 18
- 18a Thallus rather fragile and thin, with a +/- undulating surface *P. sumatrana* (atypical populations)
- 18b Thallus robust, usually with large lobes; surface never or hardly undulating *P. sumatrana* (typical populations)
- 19a Thallus robust, not distinctly undulating; lower surface with a dense network of unraised, dark veins with distinct rather small, elliptical, whitish interstices; upper surface usually with pruina at the lobes margins and sometimes with large and conspicuous incrustated patches; dolichorrhizin as the main terpenoid produced; terricolous..... *P. nana*
- 19b Thallus fragile, with a distinctly undulating surface with shallow depressions, at least in well-developed specimens; lower surface with a loose network of raised, pale to dark veins with large, elliptical, whitish to pale orange interstices; terpenoids produced in several chemotypes; mostly epiphytic, rarely on rotten wood or on terricolous mosses... 20
- 20a Dolichorrhizin abundantly produced..... *P. dolichorhiza* s. lat. **D**
- 20b Dolichorrhizin not detected..... 21
- 21a Terpenoids include zeorin and peldidactylin..... *P. dolichorhiza* s. lat. **A**
- 21b Terpenoids unknown (four produced) including a green and a red spot on TLC plates *P. dolichorhiza* s. lat. **C**

Phytogeography

Because of its wide range of well-preserved habitats, the island of New Guinea (Irian Jaya and Papua New Guinea) is expected to be a hotspot for lichen biodiversity (Sipman and Aptroot, 2006). We nevertheless consider the total number of *Peltigera* species present in Papua New Guinea as rather low (15 species accepted in this survey), especially when compared with the higher number of species in closely related genera such as *Pseudocyphellaria* (25 species mentioned from Papua New Guinea in Galloway, 1994), and with the number of *Peltigera* species reported from other parts of the world. For example 20 species of *Peltigera* are reported from Belgium and Luxembourg (Sérusiaux *et al.*, 2004), 29 from the European continent (Vitikainen, 1994), and 28 species (plus several putative ones) from British Columbia/Canada (Goward *et al.*, 1995, Miadlikowska and Lutzoni, 2000). We could not find any collections of *Peltigera canina*, *P. horizontalis*, *P. laciniata*, *P. malacca*, *P. polydactylon* and *P. tomentosa*, all species reported from New Guinea by Strei-

mann (1986: 96-98), and all are thus excluded from the flora of the island.

Martínez *et al.* (2003) summarized geographical distribution patterns of the genus throughout the world and commented on the paucity of records in S-E Asia and Australia. It is thus quite difficult to assess the endemism level reached by the genus on the whole island of New Guinea. Almost no data are available for nearby tropical mountains, especially in Indonesia and the Philippines, but it can be expected that several species newly described here have a wider distribution in those parts of the world. This is clearly suspected with the resurrection of several epithets introduced by Vainio or Gyelnik for species found in Papua New Guinea and that were virtually unknown beside their type collections: *P. erioderma* Vain., *P. nana* Vain., *P. oceanica* Gyeln. (all three described from Luzon/The Philippines) and *P. sumatrana* Gyeln. (described from Sumatra/Indonesia).

Our current understanding of the taxonomy and distribution of species leads, however, to the following observations: (1) no species of *Peltigera* is strictly pantropical; widespread species seem to be subcosmopolitan (e.g. *P. didactyla*) or if pantropical then they are also present in some temperate areas of either hemispheres (e.g. *P. ulcerata*); (2) no species is disjunct between the Neotropics and Papua New Guinea, whereas at least one species (e.g. *P. cichoracea*) could be broadly paleotropical as it is known in East Africa, Taiwan and Papua New Guinea; (3) genuine endemic species most probably exist, such as the very typical and conspicuous *P. fimbriata*; (4) putative endemic species (e.g. *P. koponenii*) likely originated from rather recent cladogenic events as suggested from the high ITS sequence similarity with their closest relative. The current data suggest that none of the species of *Peltigera* on the island are relictual species (i.e., paleoendemics).

The species

Peltigera cichoracea Jatta, Nuov. Giorn. Botan. Ital. 14: 170, 1882. (Figs 3 A-B)

Type: 'Africa, [Ethiopia] Scioa, inter muscos' (? FI, type not found).

Thallus large, in suitable conditions forming large rosettes of to 10 cm in diam., usually appressed to its substrate; lobes imbricate and divided, 0.5-1.5 cm wide with an ascending, undulate to crenate and crisped margin. *Upper surface* orange to dark brown, sometimes very dark brown, glabrous, smooth and shiny, very rarely incrustated in patches, with transversal, longitudinal or irregular cracks in mature and old parts of the thallus, exposing the medulla and with +/- raised edges and margins occasionally with isidoid granules in old thalli, but never forming schizidia. *Soralia* or *isidoid granules* or *small branched phyllidia* mixed up with thallus fragments typically formed at the lobe margins, where the cortex is typically broken and disrupted into irregular fragments, sometimes present along laminal cracks. *Lower surface* typically orange near the lobes extremities, soon becoming greenish brown, dark brown, sometimes almost black, and without veins, interstices white elliptical, sometimes numerous near lobes margins but hardly present in old parts. *Rhizines* few or abundant, fasciculate to densely branched and bush-like, black except at their tips which can be much paler. *Apothecia* rare, developed on short lateral lobes, with a dark reddish brown, circular or ellipsoid (c. 0.3 mm in diam. or c. 0.3-0.5 × 0.4 mm, in few cases reaching 0.6 x 0.5 mm), horizontal disc and a scabrid to verrucose lower side. *Ascospores* fusiform, with acute ends, mostly straight, 3-septate, (34-)35-42(-52) × 6-8 μm. *Pycnidia* not seen.

TLC: tenuiorin, methylgyrophorate, gyrophoric acid and zeorin mostly abundant (other terpenoids present include peltidactylin and dolichorrhizin but always in traces).

Nomenclature: The type collection of *P. cichoracea* could not be located in FI and is presumably lost; neotypification may be needed. The epithet is used here following the interpretation of Swinscow and Krog (1988: 200) for East Africa.

Ecology and distribution: *Peltigera cichoracea* is a conspicuous feature of the epiphytic flora of montane and subalpine forests between 2300 and 3600 m and artificial habitats like gardens hedges. It is also common on trunks of treeferns in a treefern forest in a

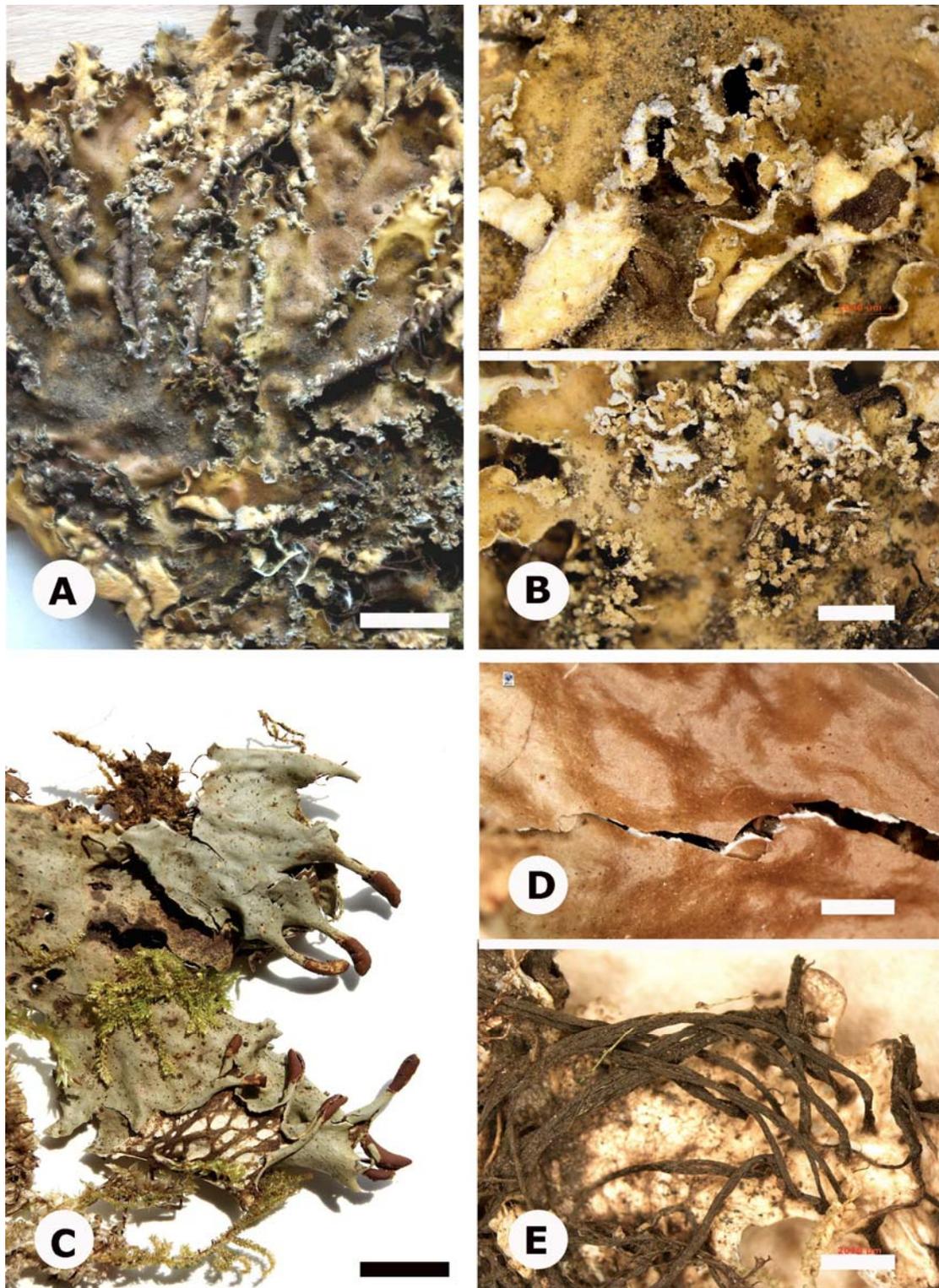


Fig. 3. **A-B.** *Peltigera cichoracea* (PNG, Teptep village, 31 July 1992, *E. Sérusiaux* s. n., LG). **A.** General habit. **B.** Details of the crisped margin with granular soredia or isidioid granules. **C, E.** *P. dolichorhiza* s. lat. **D** (PNG, Mt Gahavisuka, 5 November 1009, *E. Sérusiaux* s. n., LG). **C.** General habit **E.** Long simple rhizines. *P. dolichorhiza* s. lat. **B** (PNG, Myola, 16 October 1995, *E. Sérusiaux* s. n., LG). **D.** Foveolate upper surface. Scales: **A, C** = 1 cm, **B, D-E** = 2 mm.

deep valley in the mountains characterized by rare but acute frosts and irregular fires. Its highest locality is at 4100 m, on soil in the alpine vegetation on Mt. Wilhelm. The species is rare in the tropical mountains of East Africa

in Ethiopia, Kenya and Tanzania (Swinscow and Krog, 1988: 200) but absent on the mountains of Rwanda (*Sérusiaux et al.*, unpublished results). It has been reported as "a common species in Taiwan" (*Aptroot et al.*,

2002: 287) and can be expected elsewhere in the tropical mountains of S-E Asia. With the data currently available, *P. cichoracea* appears to be the vicariant of *P. elisabethae* for montaneous zones in the Paleotropics. Based on early results of the present study, *P. cichoracea* has been reported from Papua New Guinea by Martínez *et al.* (2003: 307).

Selected specimens examined (out of 56 collections): **Papua New Guinea: Madang prov.**, Huon Peninsula, Finisterre range, Yupna valley, Teptep village, trail in NNW and deep valley in N direction, 5°57'S 146°33'E, 2500 m, 30 July 1992, disturbed montane forest, *P. Diederich* 10796 (hb Diederich) & *E. Sérusiaux* s. n. (LG, 2 collections). **Morobe prov.**, Cromwell Mts, 7 km SE of Indagen airstrip, 147°16'E 6°18'S, ca. 2450 m, 19 June 1981, open grassland ('kunai') with scattered treeferns and sinkholes in limestone, on trunk of treefern, *T. Koponen* 31066 (H). **Northern prov.**, Owen Stanley Range, Myola, c. 3 km NE of guest house, 9°08'S 147°47'E, 2700 m, 16 October 1995, in treefern grassland in deep valley (frost hollow), *E. Sérusiaux* 15305 (LG) & *H. Sipman* 38334 (B). *Ibid.*, English Peaks, 3600 m, August 1988, *P. Lambley* 17762 (BM). **Simbu prov.**, Mt. Wilhelm, Pindaunde valley, near the hut on the S-shore of lake Piunde, 145°03'E 5° 47'S, 3600 m, 5 August 1992, subalpine forest remnants on W-slope of valley, *E. Sérusiaux* 13983 (LG). *Ibid.*, along track to the summit, 145°03'E 5°47'S, 4100 m, 7 August 1992, on soil in alpine vegetation, *A. Aptroot* 31560 (hb Aptroot). **Southern Highlands prov.**, Mt. Giluwe, 2 km E of the summit, 143°53'E 6°05'S, 4000 m, 12 September 1982, subalpine grasslands with scattered shrubs, on the ground, *H. Streimann* 24310 (CANB).

Notes: ITS sequences reveal that *P. cichoracea* belongs to Sect. *Horizontales* sensu Miadlikowska and Lutzoni (2000; Fig. 1). This paleotropical species is more closely related to *P. elisabethae* than to *P. horizontalis* (MPIBS=82%). Swinscow and Krog (1988: 200-201) suggested that *P. cichoracea* may be considered the sorediate counterpart of *P. polydactyloides* Nyl., a species so far known only from mountains of tropical Africa. The ITS sequence of a population recently collected on the volcanoes of Rwanda confirms the results of Miadlikowska and Lutzoni (2000) that *P. polydactyloides* is a member of the *P. neckeri*-clade within Sect. *Horizontales*. *Peltigera cichoracea*, *P. elisabethae* and *P. horizontalis* differ primarily in their reproductive mode. All develop apothecia, but *P. elisabethae* also produces schizidia and *P. cichoracea* is sorediate. Although it is possible that reproductive strategies are poor species

descriptors as has been shown in other species aggregates (Buschbom and Barker, 2006 for *Porpidia* s. lato), and hence that these three taxa should be considered conspecific in the light of weak differentiation in their ITS sequences, we reject this hypothesis. Indeed, differences in vegetative morphology, primarily in the venation, seem to correlate with reproductive characters (Swinscow and Krog, 1988; Vitikainen, 1994; Goward *et al.*, 1995). The lack of resolution in the ITS may be indicative of lack of cladogenesis but is not sufficient to reject our taxonomic hypothesis, which must be tested further across a broad geographic range and based on extensive genetic character sampling.

Peltigera cichoracea is a large, usually sterile species with a smooth and shiny upper surface, easily recognized by its very much disrupted, crisped margin with granular soredia, isidioid granules or small phyllidia; cracks in the upper cortex are frequent and can also help for its identification. The closely related *P. elisabethae* Gyeln. is distinguished by its typically crisped or curled schizidia, formed on the upper surface, usually near the margins (schizidia never formed in *P. cichoracea* although cracks occur frequently on the upper surface). *Peltigera horizontalis* lacks specialized vegetative propagules, and further differs from the sympatric *P. elisabethae* by the network of typically distinct veins.

Peltigera didactyla (With.) J.R. Laundon, Lichenologist 16: 217, 1984.

Type: Great Britain, "West Yorkshire, Rombalds Moor" (see Laundon 1984: 217; original description and material cited from OXF not seen).

Thallus formed of small orbicular lobes, 0.5-0.8 mm in diam with slightly ascending margins when young, becoming strongly ascending with almost vertical apothecia and then forming large rosettes to 2 cm in diam. *Upper surface* pale grey to greyish brown, with an appressed tomentum made of tiny hairs usually present at least on lobes margins, sometimes almost absent in mature lobes bearing apothecia. *Soralia* typically present on young orbicular lobes, laminal and rounded, discrete or confluent, with whitish to bluish soredia, disappearing or inconspicuous on mature lobes

bearing apothecia. *Lower surface* with distinct, raised, pale orange to whitish, anastomosing veins, leaving distinct interstices. *Rhizines* usually few, simple to rarely branched and bush-like, whitish to pale brown. *Apothecia* present on mature lobes, almost vertical, saddle-shaped, with a red brown disc, and a denticulate margin. *Ascospores* fusiform, with acute ends, almost straight, 3-7 septate, 55-70 (-77) × 4-5 μm. *Pycnidia* not seen.

TLC: no substances detected.

Nomenclature: The epithet introduced by W. Withering has been studied in detail by Laundon (1984), who synonymized the well-known *P. spuria* (Ach.) DC. with *P. didactyla* (With.) J.R. Laundon.

Ecology and distribution: A rather rare species, found on humus and gravel, between 2380 and 4200 m elevation. The populations discovered in Papua New Guinea show almost the complete variation found in the Northern hemisphere. Thalli with small, sterile orbicular lobes with laminal soralia have been found at high elevation (3600-4200 m), whereas specimens with exuberant, fertile erect lobes with only scars of eroded soralia are found lower down (2380-3250 m). The species was reported from Papua New Guinea by Streimann (1986: 97), under *P. spuria*, but the corresponding material has not been examined.

Specimens examined: **Papua New Guinea**: **Morobe prov.**, Mt. Sarawaket Southern Range, 4 km SE of Lake Gwam, headwaters of Busu River, 147°09'E 6°21'E, 3250 m, 6 July 1981, dry stream bed in open grassland, on humus, *T. Koponen* 32182 (H, LG). **Simbu prov.**, Mt. Wilhelm, 145°00'E 5°45'S, 4200 m, July 1967, on soil on summit track, *D. McVean* 6791 (CANB). *Ibid.*, Pindaunde valley, near the hut on the shore of lake Piunde, 145°03'E 5°47'S, 3600 m, 5 August 1992, subalpine forest remnants, *P. Diederich* 10198 (hb Diederich). **Southern Highlands prov.**, Mt. Giluwe, 143°50'E 6°05'S, 4110 m, 1967, wet heath on ridge, *D. McVean* 67143 (CANB). **Western Highlands prov.**, Minj-Nona Divide, Kubor Range S of Minj, 2380 m, 10 September 1963, advanced regrowth of lower montane forest, on dead tree stump, *R. Pullen* 5403 (CANB).

Notes: *Peltigera didactyla* belongs to a five-species aggregate studied by Goffinet *et al.* (2003). It is characterized by its simple or rarely branched and usually few rhizines, a tomentose upper surface (at least at the margins of young lobes) and the absence of terpenoids and depsides. The ITS sequence of a representative collection from Papua New Guinea confirms its identification (Fig. 2). Two

other species of that group occur in Papua New Guinea: *P. extenuata* that differs by its abundant and branched rhizines, and *P. ulcerata* that is characterized by its shiny, etomentose and brown upper surface and its laminal to marginal soralia.

Peltigera dolichorhiza (Nyl.) Nyl., Flora 57: 71, 1874. (Figs 3, C-E)

Type: 'Nova Granata' [Colombia], Bogotá, 2600-2700 m, 1860 (?), *Lindig* 2519 p. p. (H-NYL. 33203—lectotype !; designated by Galloway 1985: 364 and accepted by Vitikainen 1988: 136).

Thallus large c. 5-7 cm across (rarely to 10 cm), sometimes rather elongate, with lobes more or less separated from each other, extremities usually rounded and 0.8-1.2 cm wide, with flat or slightly revolute margins; thalli rather fragile and easily broken apart when dry. *Upper surface* glabrous, beige, orange to dark brown, or bluish grey, smooth and usually rather shiny, without tomentum or pruina, usually distinctly undulating with uneven but distinct depressions. *Lower surface* pale orange to brownish near the margins, becoming dark brown to blackish, with a network of slightly raised, blackish veins, with large, numerous, usually elliptical, whitish to pale orange interstices, forming an attractive design, with a thin, araneous, orange to blackish layer of hyphae covering them, especially near the margins. *Rhizines* abundant, usually quite long (to 0.8-1 cm long), simple or penicillate, exceptionally fasciculate, sometimes quite thick (c. 0.3 mm in diam.). *Apothecia* absent or rare, on rather narrow, +/- raised, digitate and strongly revolute lobes, to 0.4-0.7 cm long (incl. the apothecial disc); disc dark reddish brown, usually saddle-shaped; margins incised. *Ascospores* (3-)7-septate, 68-102 × 4.5-5 μm. *Pycnidia* not seen.

Notes: *P. dolichorhiza* is an epithet usually applied to tropical populations with a thin and rather fragile thallus, smooth upper surface usually uneven and with distinct depressions, raised and digitate apothecia, pale orange lower surface near the margins, distinct network of white elliptical interstices over a dark background towards the center of the thallus, simple and long rhizines and production of several terpenoids. Our ITS sequences

demonstrate that specimens with such characters (or slightly differing by their size and rhizines branching pattern) belong to two well supported clades forming a paraphyletic entity (Fig. 1). No morphological or chemical characters can differentiate the two lineages. The type material of *P. dolichorhiza* contains dolichorrhizin (large spot by TLC), and may be identical to accessions *P. dolichorhiza* 13 & 14 in Clade 1, which both produce this terpenoid, whereas all remaining accessions lack this compound and are resolved within the well-supported Clade 2. However several collections from Rwanda (Africa) produce dolichorrhizin in significant quantities but unambiguously fall in Clade 2 (Goffinet & Sérusiaux, unpubl. results). In the material from Papua New Guinea, Clade 2 comprises three distinct chemotypes and at least one of them is morphologically distinct (*P. dolichorhiza* s. lat. B).

As discussed above (§ Phylogenetic analysis of ITS sequences), further data must be obtained before a final decision can be taken on the taxonomical and nomenclatural status of material here referred to *P. dolichorhiza*.

Several collections of *P. dolichorhiza* were mentioned from Papua New Guinea by Streimann (1986: 97) but none have been examined by us.

***Peltigera dolichorhiza* s. lat. A**

TLC: tenuiorin, methylgyrophorate, gyrophoric acid and terpenoids present include peltidactylin (sometimes absent) and zeorin.

Ecology and distribution: *Peltigera dolichorhiza* s. lat. A occurs as an epiphyte in montane forests within a narrow altitudinal range between 2500-2900 m elev.

Specimens examined (out of 13 collections): **Papua New Guinea, Madang prov.**, Huon Peninsula, Finisterre range, Yupna valley, Teptep village, trail in NNW and deep valley, 5°57' S 146°33'E, 2500 m, 30 July 1992, disturbed mountain forest, *E. Sérusiaux* 13622 (LG). **Simbu prov.**, Mt. Wilhelm area, Bundi Gap, on road Keglsugl-Bundi, 5°48'S 145°09'E, 2800 m, 4 August 1992, subalpine forest remnants, *P. Diederich* 11052 (hb Diederich).

***Peltigera dolichorhiza* s. lat. B**

TLC: tenuiorin, methylgyrophorate, gyrophoric acid and terpenoids: zeorin and at least one unknown (in between dolichorrhizin and zeorin positions in G).

Ecology and distribution: Most of the collections of *P. dolichorhiza* s. lat. B have been found in a single locality, on treefern trunks in a treefern forest, in a deep valley in the mountains characterized by rare but acute frosts and irregular fires. The second locality was also made on the trunk of a treefern, in the Huon Peninsula. The altitudinal range is 2700-3250 m.

Specimens examined: **Papua New Guinea: Northern Prov.**, Owen Stanley Range, Myola, c. 3 km NE of guest-house, 9°08'S 147°47'E, 2700 m, 16 October 1995, in treefern grassland in deep valley (frost hollow), *E. Sérusiaux* (LG; 3 specimens collected on 3 different treefern "trunks") & *H. Sipman* 38337 (B). **Morobe prov.**, Mt. Sarawaket Southern Range, 4 km SE of Lake Gwam, headwaters of Busu R., 6° 21'S 147°09' E, 3250 m, 6 July 1981, subalpine forest on steep SW-facing slope, on trunk of treefern, *T. Koponen* 32070 (H).

Notes: *Peltigera dolichorhiza* s. lat. B differs from typical *P. dolichorhiza* by its larger thalli (up to 15 cm across), with large lobes, 1-1.8 cm wide, smooth and shiny upper surface, rhizines few or sometimes abundant, penicillate to fasciculate, and a unique chemistry (zeorin and at least one unidentified terpenoid). Amongst other species in Papua New Guinea, it is similar to *P. sumatrana* which has the same morphological features except for the more common, typically saddle-shaped apothecia and a different chemistry (dolichorrhizin always present and abundantly produced). *P. sumatrana* is resolved into Clade 1, whereas three accessions of *P. dolichorhiza* s. lat. B (all coming from a single locality) form a well-supported clade nested within the poorly resolved Clade 2.

A morphologically similar collection (*Koponen* 32070) is tentatively assigned to this species but it produces peltidactylin and zeorin.

***Peltigera dolichorhiza* s. lat. C**

TLC and HPLC (made by J. A. Elix): tenuiorin, methyl gyrophorate, methyl lecanorate, methyl evernate, methyl orsellinate, and four unknown terpenoids (easily recognized on TLC plates as they include a green and a red spot).

Ecology and distribution: *Peltigera dolichorhiza* s. lat. C exhibits a wide altitudinal range in Papua New Guinea as it has been primarily collected between 1850 and 3600 m with one sample occurring at 4420 m on Mt. Wilhelm. It mostly grows on mossy trees in

montane forests, but can also colonize humus rich ground, dead stumps and ground mosses.

Selected specimens examined (out of 36 collections): **Papua New Guinea, Eastern Highlands prov.**, Mt. Gahavisuki Provincial Park, 11 km N of Goroka, 145°25'E 6°01'S, 2300 m, 17 Mar 1987, epiphyte in disturbed mossy mountain forest, *H. Sipman* 22199 (B). *Ibid.*, 2400 m, 3 August 1992, little disturbed mossy mountain forest, *P. Diederich* 10582 (hb Diederich). *Ibid.*, 2300 m, 5 November 1995, little disturbed mossy mountain forest, dominated by *Castanopsis*, *E. Sérusiaux* s. n. (LG). **Madang prov.**, Huon Peninsula, Finisterre Range, Yupna valley, Teptep village, towards Bambu airfield, 146°33'E 5°57'S, c. 2600 m, 30 July 1992, burnt forest with scattered old trees and regrowth, *E. Sérusiaux* s. n. (LG), *H. Sipman* 35311 (B). Huon Peninsula, 2 km NW of Teptep Airstrip, 146°33'E 5°56.5'S, 2450-2700 m, 28 July 1981, heavily cut montane rainforest on SE-sloping ridge, on trunk of *Pandanus*, *T. Koponen* 34738 (H). *Ibid.*, 4 km NW of Teptep Airstrip, 146°32.5'E 5°36'S, 2800-2900 m, 28 July 1981, slightly disturbed montane rainforest on ridge, on stump, *T. Koponen* 34691 (H). **Morobe prov.**, Mt. Kaindi Road, 4 km W of Wau, 146°40'E 7°21'S, 2100 m, 21 June 1979, *Nothofagus-Phyllocladus* dominated forest, on rotting trunk, *A. Kairo* 363 (H). **Northern prov.**, Owen Stanley Range, Myola, 0-1 km along trail from guesthouse towards NE, on the right bank of Iora river, 147°46'E 9°09'S, 2100-2400 m, 15 October 1995, primary mountain forest on mountain slope, *E. Sérusiaux* s. n. (LG, 2 collections) *H. Sipman* 38261 (B). **Simbu prov.**, Mt. Wilhelm, 145°00'E 5°45'S, 4420 m, July 1967, on moss near summit, *D. McVean* 67111 (CANB). **Southern Highlands prov.**, Onim Forestry Station, 14 km NNW of Ialibu, 143°59'E 6°09'S, 2250 m, 14 September 1982, edge of disturbed montane forest and grasslands, base of young *Nothofagus*, *H. Streimann* 24549 (H). **Western Highlands prov.**, N slopes of Sugarloaf complex (along Wapu River), 2790 m, 15 July 1960, montane cloud forest, epiphytic on moss, *R. D. Hoogland & R. Schodde* 7085 (CANB).

***Peltigera dolichorhiza* s. lat. D**

TLC: tenuiorin, methylgyrophorate, gyrophoric acid and terpenoids present include peltidactylin (sometimes absent), dolichorhizin (always present and produced in large quantities) and zeorin.

Ecology and distribution: *P. dolichorhiza* s. lat. D is an epiphytic species found in montane forests between 1800-2400 m elev., not detected among the plentiful material collected at higher elevations.

Selected specimens examined (out of 18 collections): **Papua New Guinea: Central prov.**, Owen Stanley Range, trail from Myola to Naduri, 147°41'E 9°08'S, c. 1800 m, 20 October 1995, montain forest remnants (with e. g. *Lithocarpus*), on tree, *E. Sérusiaux* s. n. (LG). **Eastern Highlands prov.**, 6 km SW of Lufa, near Hogabi village, 145°16'E 6°21'E, 1850 m, 14 April

1982, montane forest ridge, *Nothofagus* dominated, on treelet, *H. Streimann* 18671 (CANB). **Morobe prov.**, Huon Peninsula, Saruwaged Range, Honzukngon village S of Derim airstrip in Timbe valley, 147°06' E 6°14'S, 2100 m, 7-8 March 1987, epiphyte in mossy mountain forest above village, on thin stem, *H. Sipman* 24434 (B). Mt. Kaindi, 4 km W of Wau, 146°41'S 7°21'S, 2350 m, 13 March 1982, dense *Nothofagus* regeneration on summit, on small tree trunk, *H. Streimann* 17671 & *A. Bellamy* (CANB).

***Peltigera erioderma* Vain.**, Philippine Journal of Science, C. Botany, 8(2): 112, 1913.

(Figs 4 A-C)

Type: Philippines, Luzon, subprov. Benguet, mons Pulog, ad truncos putridos arborum et ad terram muscosam, s. d., "*For. Bur. 16362 Curran, Merrit & Zschokke, Bur. Sci. 8936 McGregor*" (TUR—Vainio 9837: specimen originally numbered 16362 with annotations by Vainio here selected as the lectotype !; BM—isolectotype !)

Thalli typically large to 10-15 cm in diam., with imbricate lobes, rounded at their extremities and 1-1.5 cm wide, margin revolute. *Upper surface* pale orange to brown but almost white in the best developed specimens, with a usually well developed and appressed tomentum made of tiny hairs (0.1-0.5 mm high) near the margins and a +/- appressed, 40-110 µm thick network of hyphae elsewhere and out of which hairs 0.1-0.4 mm long, sometimes aggregated in small emerging tufts; in specimens growing in less suitable conditions, tomentum appressed (without erecting hairs) irregularly scattered and mainly present on young lobes and those carrying apothecia. *Lower surface* whitish to pale brown, becoming almost black towards the center in old specimens, usually with the medulla hyphae easily seen under the dissecting microscope, with a distinct and well-developed network of large (0.3-0.7 mm), raised, and soon dark brown to black veins, which are densely anastomosing; interstices between the veins usually covered by an araneous blackish layer near the margins. *Rhizines* simple, threadlike to fasciculate and rarely bushy, pale near the margins but soon dark brown to black, sometimes very long, usually not very abundant. *Apothecia* usually present, typically horizontal, developed on swollen lateral lobes; disc dark reddish brown, remaining concave or becoming flat when mature, ellipsoid, to 6.5 × 4 mm in diam.,

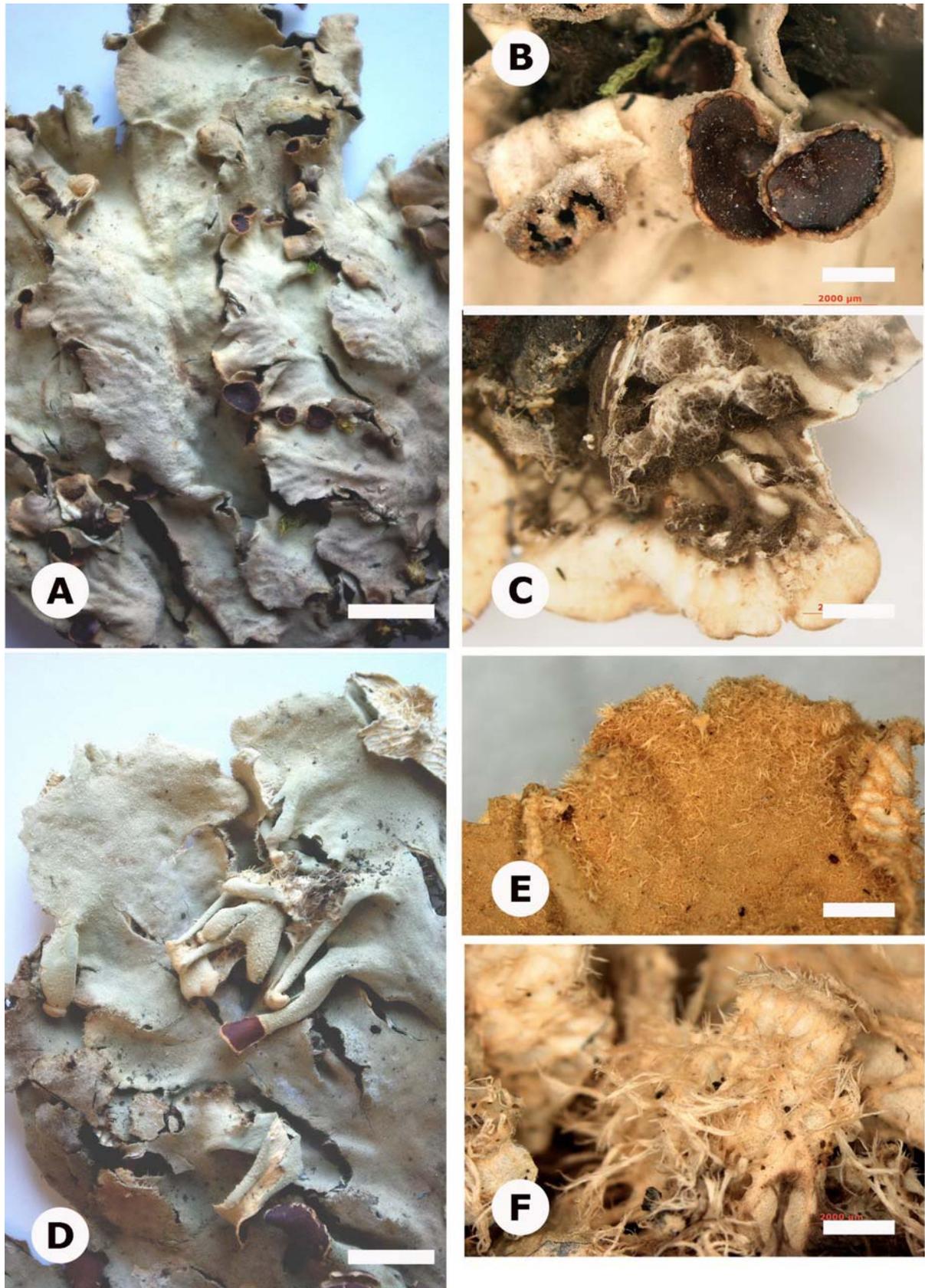


Fig. 4. A-C. *Peltigera erioderma* (PNG, Myola, 16 October 1995, E. Sérusiaux s. n., LG). A. General Habit. B. Young horizontal apothecia. C. Fasciculate rhizines near the edge of the lobes. D-F. *P. fimbriata* (PNG, T. Koponen 32996, LG—isotype). D. General habit. E. Hairs over the upper surface. F. Rhizines. Scales: A, D = 1 cm, B-C, E-F = 2 mm.

margins slightly incised, rarely crenulate; lobes carrying the disc distinctly tomentose. *Ascospores* fusiform to acicular, straight or slightly curved, 3(-5)-septate, with rather rounded ends, (51)-60-75 × 4-5(-6) μm (one abnormal spore with 11 septa and 90 × 5 μm seen). *Pycnidia* absent or very rare, present on lobes margins, sessile, black, globose, 0.1-0.3 mm in diam., with a central ostiole; conidia not seen.

TLC: no substances detected.

Nomenclature: Two collections are mentioned in the protologue (n° 16362 and 8936) and both are in TUR and BM. The specimen originally numbered 16362 in TUR has handwritten annotations by Vainio and is here selected a lectotype.

Ecology and distribution: *Peltigera erioderma* is a rare, epiphytic species growing on mosses in the montane and subalpine forests between 2700 and 3400 m; it is known only from the Mt. Wilhelm area and a treefern forest in a deep valley submitted to rare but acute frosts and irregular fires in the Northern prov. It was reported from New Guinea by Streimann (1986: 97) and by Martínez *et al.* (2003: 307).

Selected specimens examined (out of 25 collections): **Papua New Guinea: Northern prov.**, Owen Stanley Range, Myola, c. 3 km NE of guesthouse, 147°47'E 9°08'S, 2700 m, 16 October 1995, on treefern trunk in treefern grassland in deep valley (frost hollow), *E. Sérusiaux* s. n. (LG, 2 collections) & *H. Sipman* 38335 (B). **Simbu prov.**, Mt. Wilhelm area, c. 11 km on new road under construction from Gembogl to Goroka, 145°09'E 5°55'S, 2800 m, 9 August 1992, mossy montane forest, *A. Aptroot* 32830 (hb Aptroot), *P. Diederich* 11105 (hb Diederich), *E. Sérusiaux* 14107 (LG). **Southern Highlands prov.**, Munia logging area, 14 km NW of Ialibu, 143°55'E 6°11'S, 2300 m, 8 September 1982, *Nothofagus* and Podocarpaceae dominated forest, on treefern stem, *H. Streimann* 23224 (CANB, H). Mt. Giluwe, 143°50'E 06005'S, 3350 m, on trees in subalpine forest, *D. McVean* 67134 (CANB).

Notes: *Peltigera erioderma* is readily identified by its large thalli with a tomentose upper surface and revolute margin, and its horizontal apothecia. *Peltigera fimbriata* also has a tomentose upper surface but it is distinguished by its saddle-shaped apothecia and much longer hairs on its upper surface [0.1-0.4 mm in *P. erioderma* vs 1(-1.4) mm in typical populations of *P. fimbriata*]. *Peltigera kopenhagenii* is another species forming large thalli with a tomentose upper surface; it differs

by its saddle-shaped apothecia and its very abundant, fibrillose to coralloid rhizines.

Peltigera montis-wilhelmii and *P. papuana* are the only other species in the Papuan flora with horizontal apothecia, the former being readily identified by the complete absence of tomentum on its shiny upper surface and the latter by its much smaller size, smooth to scabrose upper surface, sometimes with a whitish pruina at the lobe margin and usually by the production of marginal phyllidia. Nevertheless, the morphological boundaries between *P. erioderma*, *P. montis-wilhelmii* and certain forms of *P. papuana* remain somewhat ambiguous (see further comments under *P. papuana*).

ITS sequences show that this species is most closely related to the very similar *P. montis-wilhelmii* that is easily distinguished by its glabrous, shiny upper surface. The shared ancestry of *P. erioderma* and *P. montis-wilhelmii* is well-supported but their affinities within the Sect. *Peltigera* are uncertain (Fig. 2).

Peltigera extenuata (Vain.) Lojka, Lichenoth. Univ., fasc. V, n 222, 1886.

Type: Finland, Tavastia australis, Asikkala, Kaitas 1863, *Silén & Norrlin* (H—lectotype!).

Thallus medium-sized, of irregularly divided lobes, 1-3 cm long and 0.5-1 cm wide, with typically rounded and concave extremities (forming attractive rounded 'cupulae' with a slightly revolute margin). *Upper surface* pale orange to brownish, in most parts with a dense, appressed and whitish tomentum. *Soralia* abundant, rounded, 0.1-0.2 mm in diam., flat or slightly concave, but slightly excavate when all soredia are gone, laminal, mostly present on young lobes on which they are +/- regularly scattered, with a distinct rim of cortex when young; soredia granular, pale orange to dark brown, usually abundant. *Lower surface* pale with a network of whitish, slightly raised but hardly delimited veins. *Rhizines* very abundant, forming a dense cushion, present up to lobe margins, pale orange or whitish, densely branched to fibrillose. *Apothecia* and *pycnidia* not seen.

TLC: methylgyrophorate and gyrophoric acid (traces) in young sorediate lobes, the soralia typically reacting C+ red.

Nomenclature: The type material has been studied by Goffinet and Hastings (1995), and their interpretation is here followed.

Ecology and distribution: Known from only one locality, on soil in alpine vegetation at 4200 m on Mt. Wilhelm. *Peltigera extenuata* has a wide distribution in the Northern hemisphere, being found mainly in arctic tundras, boreal and montane forests overgrowing mosses on soil or on rocks, as well as in disused quarries and other disturbed localities in the temperate zone. In Asia, it is known from a single locality in Northern China (for more details, see Goffinet and Hastings, 1995: 48-54). It is reported from New Zealand as a “chemodeme” of *P. didactyla* by Galloway (2000, 2007). It is new for Papua New Guinea.

Specimen examined: Papua New Guinea: Simbu prov., Mt. Wilhelm, Pinaunde valley, along track to the summit, 145°03'E 5°47'S, 4200 m, 7 August 1992, on soil in alpine vegetation, A. Aptroot 33118 (hb Aptroot).

Notes: This taxon was resurrected by Goffinet and Hastings (1995), and distinguished from the subcosmopolitan *P. didactyla* by its abundant and densely branched to fibrillose rhizines, and the occurrence of methylgyrophorate and gyrophoric acid in young sorediate lobes and soredia. Recent studies based on nrDNA sequences clearly demonstrate its species status (Goffinet *et al.*, 2003). The single collection from Papua New Guinea matches that description very well.

Peltigera fimbriata Vitik., Sérus., Goffinet & Miádl. **sp. nov.** (Fig. 4 D-F)
MycoBank: 513027

Etymology: This very spectacular species is named after its most obvious character, the long hairs that grow on its upper surface.

Ab aliis speciebus *Peltigerae* differt thalli superna facie tomentosa et pilis numerosis et longis instructa.

Type: Papua New Guinea, Morobe prov., between Mt. Sarawaket Southern Range and Iloko village, 2 km SW of Iloko, 147°10'E 6°06'S, 1800 m, 11 July 1981, along stream in montane rainforest, on boulder, T. Koponen 32996 (H—holotype, LG—isotype).

Species forming large colonies to several m² in suitable localities, with large thalli to 20-30 cm across, and lobes to 1-1.5 cm wide, with a revolute margin. *Upper surface* pale grey or orange brown to greyish, sometimes almost white when tomentum and hairs are very abundant, with a thick and dense whitish tomentum

that usually covers it all but sometimes scarce or even absent, rarely incrusting in patches, with threadlike, whitish to pale orange, rarely pale brown, hairs, to 1 (-1.4) mm long, that are usually abundant and forming tufts or ‘bushes’ mainly near the margins and lobes extremities (when rare, mostly present in such positions), rarely absent in specimens with abundant apothecia. *Phyllidia* very rare, produced at the margins of regenerating old lobes. *Lower surface* pale orange, with a network of strongly raised veins which are pale orange near the margins but soon become dark brown to black, leaving large ellipsoid interstices. *Rhizines* abundant to extremely abundant and then forming cushions or fluffy masses under the thallus, simple, penicillate or less frequently fasciculate, often confluent, at first pale orange but soon dark brown (at least in parts). *Apothecia* absent or abundant, growing almost vertically on digitated, raised and almost completely revolute lobes (to 1.5 cm long, incl. apothecial disc); disc dark reddish brown, saddle-shaped and elongate, 3-5 mm long with a slightly raised, usually smooth margin. *Ascospores* 5-7-septate, acicular with +/- rounded ends, straight, 65-80 × 3.5-4 μm. *Pycnidia* almost always present (albeit sometimes quite few) on lobes margins, sessile, black, globose, sometimes pyriform, conspicuous because of their size (0.3-0.8 mm in diam.), with a central, apical ostiole which is wide open in old and empty ones; no conidia seen (although c. 15 pycnidia examined).

TLC: no substances detected.

Ecology and distribution: *Peltigera fimbriata* forms large and conspicuous thalli that are primarily terricolous, growing on gravel by rivers or streams, on bare earth in recent landslides and on soil in grasslands. It is locally abundant in the montane zone, but has also been found in the subalpine and alpine zones. It also grows on artificial habitats like shaded road banks. In New Guinea *P. fimbriata* exhibits the broadest altitudinal range (from 1300 to 4145 m elev.) among *Peltigera* species.

Selected specimens examined (out of 55 collections): Papua New Guinea: Enga prov., Mt. Hagen-Wabag road, 18 km SE of Wapenamanda, 143°58'E 5°47'S, 2700 m, 27 June 1982, advanced regrowth on slope, on the ground in semi-exposed road cutting, H. Streimann 21268 (CANB). Madang prov., Huon Peninsula, Finisterre range, Yupna valley, Teptep

village, trail in NNW and deep valley in N direction, 5°57'S 146°33'E, 2500 m, in disturbed montane forest, gravel slopes along stream, 30 July 1992, *P. Diederich* 10984 (hb Diederich). **Morobe prov.**, Aseki-Mdamna Track, 1 km SW of Aseki, 7°22'S 146°10'E, 1350 m, 22 January 1981, on shaded moist rock, rocky area besides stream, advanced secondary vegetation besides large stream in deep gorge, *H. Streimann* 12520 (B, CANB, H). Saruwaged Range, Honzeukngon village S of Derim in Timbe valley, 147°06'E 6°13'S, 1850 m, March 1987, on soil in gardens, *A. Aptroot* 17784 & 17788 (hb Aptroot). Aseki-Menyama road, 146°06'E 7°16'S, 1910 m, 21 January 1981, cleared area through montane forest, on moist and shaded road side, *H. Streimann* & *E. Tamba* 12225 (CANB, H). **Simbu prov.**, Mt. Wilhelm, near the hut on the S-shore of lake Piunde, 145°03'E 5°47'S, 3500 m, 12 March 1987, subalpine grassland and shrubs on bottom of valley, *H. Sipman* 21967 (B). **Southern Highlands prov.**, Tari Gap, 29 km ESE of Tari, 143°11'E 5°56'S, 2560 m, 17 December 1982, on soil bank bordering grassland, *J. A. Elix* 13338 & *H. Streimann* (CANB). **Western Highlands prov.**, Al River valley, NW of Nondugl, 2000 m, 3 April 1953, on rock in broad creek, sunny, slightly above water level, *R. D. Hoogland* 3216 & 3217 (CANB). **Indonesia, Irian Jaya:** Carstensz Mts, 10 December 1971, *G. Hope* CGE L6 (COLO). *Ibid.*, Upper Meren Valley, 4145 m, 30 December 1971, terrestrial on fresh moraines, in moist flat exposed area, *G. Hope* CGE L38 (CANB).

Notes: Phylogenetic inferences from 5.8S and ITS2 sequence suggest that *P. fimbriata* shares a common ancestor with the allopatric and morphologically distinct *P. ponojensis* and *P. monticola* (both northern temperate species) but support for this hypothesis is lacking (Fig. 2).

Peltigera fimbriata is the most readily recognized species in the Papuan flora as its tomentose upper surface harbors long whitish hairs, in particular along the lobes margins, that furthermore almost invariably carry black pycnidia. The species is especially common in the Huon Peninsula at c. 2300-2700 m elev. where it grows intermingled with *P. koponenii*. The latter is easily distinguished by the absence of whitish hairs and black pycnidia and by its fibrillose to coralloid rhizines.

The neotropical *P. laciniata* (G. Merr. ex Riddle) Gyeln. (Vitikainen, 1998) is distinguished by its much smaller thallus and narrower lobes (usually less than 0.5 mm wide near the extremities), the absence of whitish hairs, the pale or almost white upper surface due to a dense tomentum, the upturned margins of its lobes, and the production of zeorin. Its rhizines are also very diagnostic as they are

quite long and squarrosely branched and fasciculate.

Several populations are assigned to *P. fimbriata* with some hesitation because the typical whitish hairs on the upper surface tend to be much shorter, in some cases are rather sparse and virtually indistinct from the tomentum, or even completely absent. Such populations also have more elongated and narrower lobes and their rhizines are usually quite numerous, typically arranged in rows on the veins (especially on young lobes) and form compact fluffy masses. They are not clearly different from the most typical *P. fimbriata* populations (for example, the conspicuous, marginal pycnidia are present) and several intermediates occur, especially in the Huon Peninsula. Our ITS sequences (*P. fimbriata* 2 and 3) do not support segregating these specimens into another taxon distinct from typical *P. fimbriata* (*P. fimbriata* 1 in Fig. 2), but more detailed studies are needed to assess the taxonomic value of the observed phenotypic variation.

Representative specimens examined: **Papua New Guinea:** **Morobe prov.**, Lake Wamba 5 km S of Teptep airstrip, Teptep-Wantuat trail 10 km S of Teptep, 146°33'E 6°2.5'S, 2550-2700 m, 24 July 1981, open montane forest, on humus, *T. Koponen* 33912 (H). **Simbu prov.**, Mt. Wilhelm, Pindaunde valley, along track to the summit, 145°03'E 5°47'S, 4000 m, on soil in alpine vegetation, 7 August 1992, *A. Aptroot* 33080 (hb Aptroot). *Ibid.*, Lake Aunde, 6 km SE of Mt Wilhelm, 145°03'E 5°46'S, 3520 m, May 1966, in tussock grassland, *D. McVean* 66137 (CANB). **Southern Highlands**, Tari Gap, 25 km SE of Tari, 5°56'S 143°06'E, 2740 m, 13 September 1982, on a gentle slope on semiexposed road cutting in montane forest, *Nothofagus* dominated, *H. Streimann* 24511 (B, CANB, H). **Indonesia, Irian Jaya:** Carstensz Mt, 10 December 1971, *G. Hope* CGE L6 p.p. (CANB).

Peltigera granulosa Sérus., Goffinet, Miädl. & Vitik. **sp. nov.** (Fig. 5 A-C)
MycoBank: 513028

Etymology: The species name refers to the typically granulose margin.

Ab aliis speciebus *Peltigerae* differt thallo friabili et sorediosa, granulosa vel isidiata margine.

Type: Papua New Guinea, Morobe prov., Kwama River valley NE of Mt. Sarawaket Southern Range, 147°12'E 6°04'S, 1700 m, 12 July 1981, along trail in open grassland between Gumum and Sape villages, on sand, *T. Koponen* 33267 (H—holotype; LG—isotype).

Thallus rather fragile, thin and usually easily broken into pieces, formed of elongated lobes with rather few divisions and with rounded and imbricate lobes, usually with an upturned, crisped margin; when growing on mossy ground, most lobes erect. *Upper surface* bluish grey, or brownish to dark brown, glabrous, smooth and rather shiny, sometimes with a whitish delicate pruina near the lobes margin, rarely with irregular cracks in old parts of the thallus. Margins, especially at the extremities of the lobes, usually dissolving into *soredioid granules*, or *isidioid fragments* (rarely with small, ill-looking phyllidia), with many tending to accumulate on the edge of the lower surface; tufts of small whitish hairs sometimes present on the margin. *Lower surface* whitish to almost pure white at the margins, remaining so or becoming blackish towards the center or in old specimens, with a network of strongly raised, dark and anastomosing veins which can be almost invisible at the margins. *Rhizines* abundant or not, rarely reaching the margins, simple, very rarely branched or fasciculate, long, blackish. *Apothecia* absent or few, developed at the extremities of erect lobes (ca. 1 cm long) which are +/- flat or slightly revolute, with a slightly convex dark reddish brown disc to 4 × 1.5 mm. *Ascospores* acicular, with rounded ends, straight or slightly curved, 5-7 septate, 53-69 × 3-4 µm. *Pycnidia* few, marginal, sessile, black, ovoid or slightly elongate, 0.3-0.5 mm; *conidia* ovoid, 6-10 × 3-4 µm.

TLC: no substances detected by TLC.

Ecology and distribution: *Peltigera granulosa* seems to be primarily a pioneer species growing on bare ground, usually sand or gravel but also on plant debris and peat, either in natural or artificial habitats (e. g. on road banks), and mossy soils in the montane forest zone. It occurs also on mossy trunks within forests where it usually develops smaller and sometimes inconspicuous individual lobes. Its localities are distributed between 1300 and 3660 m elev.

Selected specimens examined (out of 26 collections): **Papua New Guinea: Eastern Highlands prov.**, Mt. Gahavisuka Provincial Park, 11 km N of Goroka, 145°25'E 6°01'S, 2300-2450 m, 11 August 1992, on soil in montane forest, A. Aptroot 32396 (hb Aptroot). **Madang prov.**, S side of Ramu valley, Bundi village, along road to Bundi Gap, 5°44,9'S 145°14,1'E,

1300 m, 9 November 1995, on roadbank among secondary vegetation, E. Sérusiaux s. n. (LG) & H. Sipman 39313 & 39346 (B). Huon Peninsula, Finisterre range, Yupna valley, Teptep village, trail in NNW and deep valley in N direction, 5°57'S 146°33'E, 2500 m, 30 July 1992, disturbed montane forest, gravel slopes along stream, P. Diederich 10875 (hb Diederich). **Morobe prov.**, Wau area, Edie Creek road, 1850 m, 5 August 1981, bank of road on grassy slope, H. Sipman 15605 & 15606 (U). **Northern prov.**, Owen Stanley Range, Myola, surroundings of guest-house, 9°09'S 147°46'E, 2100 m, 14-19 October 1995, gravel deposits along Iora creek, E. Sérusiaux 15150 (LG). **Simbu prov.**, Lake Aunde, 6 km SE of Mt. Wilhelm, 145°03'E 5°46'S, 3660 m, May 1966, on mossy rock, D. McVean 66180 (CANB, COLO). **Western Highlands prov.**, Kubor Range, Nona River, 1910 m, epiphytic on tree-base hanging over river, secondary growth, 4 September 1963, W. Vink 16486 (hb Aptroot).

Notes: *Peltigera granulosa* belongs to Sect. *Peltigera*, and most likely to the *P. rufescens*-group (Fig. 2; Miadlikowska *et al.* 2003). Recoded INAASE and arc characters helped to define it as a monophyletic lineage (MPIBS = 91%), closely related to the sympatric *P. papuana*, and the allopatric neotropical *P. laciniata* (MPIBS=82%). Two monophyletic groups were detected but these are indistinguishable morphologically.

Peltigera granulosa is easily recognized by its rather fragile thallus with a smooth upper surface, a soredioid, granulose to isidioid margin, lack of chemistry and strongly raised veins with long and simple rhizines (when fully-developed). These features easily distinguish it from its closest relatives.

***Peltigera koponenii* Sérus., Goffinet, Miadl. & Vitik. sp. nov.** (Figs 5 D-F)
Mycobank: 513029

Etymology: This new species is dedicated to Dr. T. Koponen who made large and well processed collections of *Peltigera* in Papua New Guinea, mainly from the Huon Peninsula.

A *Peltigera canina* differt rhizinis numerosissimis, fibrillosis et coralloidibus.

Type: Papua New Guinea, Morobe prov., Lake Wamba 5 km S of Teptep airstrip, 146°34'E 6°0.5'S, 2400-2500 m, 26 July 1981, open montane *Nothofagus-Pandanus* forest on ridge, on trunk, T. Koponen 34327 (H—holotype, LG—isotype).

Species forming large *thalli* up to 20 cm in diam., with elongate lobes (to 6-7 cm long) sparingly divided, with rounded lobes 0.5-0.8 mm wide at the extremities, and with a revolute

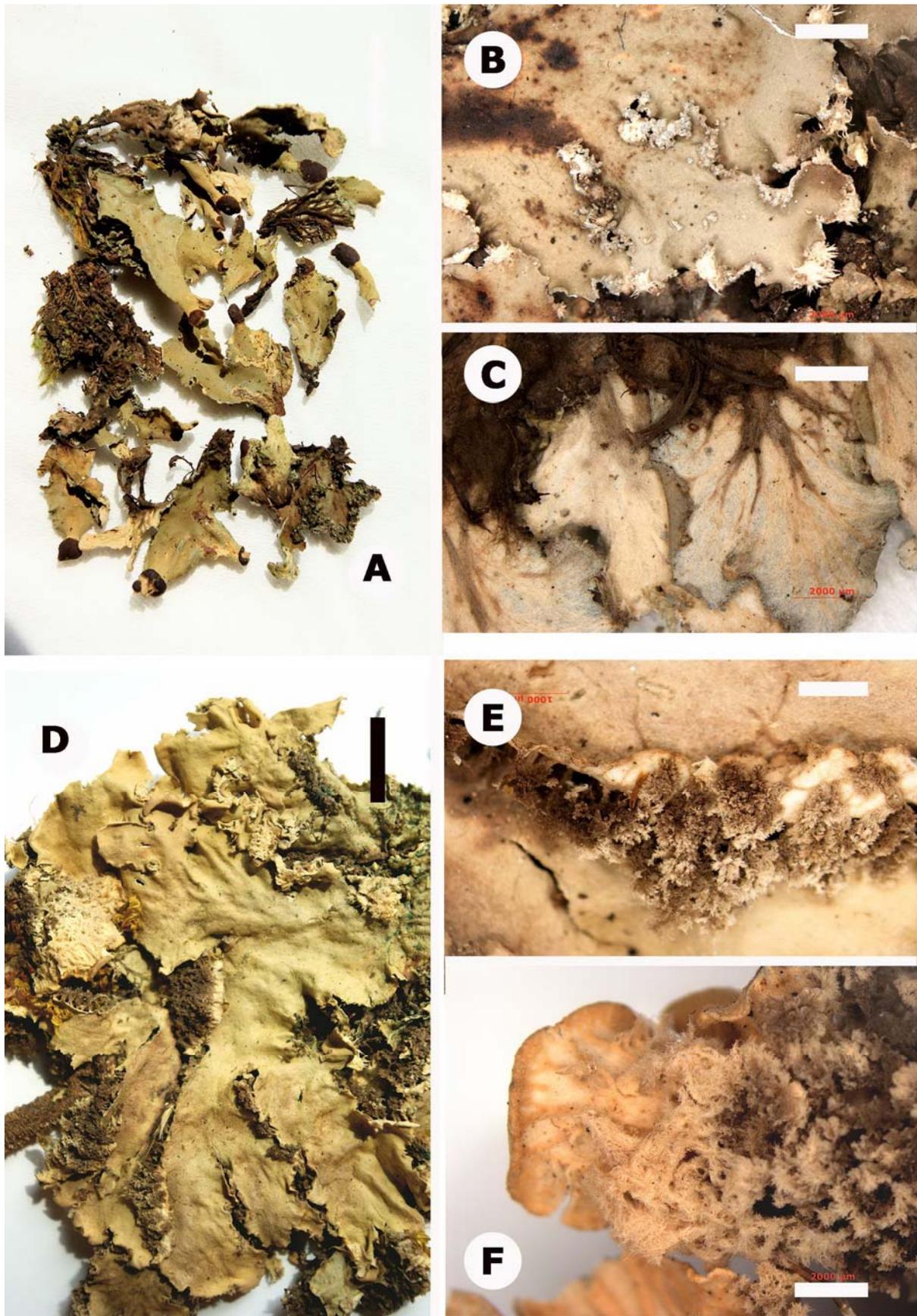


Fig. 5. A-C. *Peltigera granulosa*. A. General habit (PNG, Sarawaket, *T. Koponen* 33267, LG—istotype). C-B (PNG, Bundi, *H. Sipman* 39346, B). B. Marginal soredioid granules (with tufts of hairs in this specimen). C. Lower surface. D-F. *P. koponenii* (PNG, Lake Wamba, *T. Koponen* 34327, LG —istotype). D. General. E-F. Rhizines and lower surface. Scales: A, D = 1 cm, B-C, E-F = 2 mm.

margin; sometimes with shorter and more imbricate lobes with their lateral margin slightly raised to crenulate. *Upper surface* pale grey, slightly orange or sometimes bluish-grey, or with dark and rather large but not delimited patches, especially towards the thallus center, with an appressed, whitish to pale brown tomentum over much of the surface, especially near lobes margin but sometimes absent; wide and longitudinal convex folds seen on all well-preserved thalli. *Lower surface* whitish to beige or pale brown, usually hardly darkened towards the center, whitish interwoven hyphae of the medulla easily seen under the dissecting microscope, with a network of pale orange to brownish, distinctly raised veins. *Rhizines* abundant to extremely abundant and then forming dense (to 5 mm thick) cushions under the thallus, typically fibrillose and soon becoming coralloid because of further branching of most lateral fibrils, or fibrillose to +/- fasciculate and forming dense 'bushy' masses, at first whitish to pale brown but soon becoming dark brown to almost black, usually long (several to 1 cm long). *Apothecia* absent or abundant, growing almost vertically on digitated, raised and revolute lobes (to 1.5 cm long, incl. apothecial disc); disc dark reddish brown, saddle-shaped and elongate, 4-5 mm long, usually with an indistinct margin. *Ascospores* 3-septate, acicular, straight, with +/- rounded ends, $44\text{--}53 \times 4\text{--}4.5 \mu\text{m}$. *Pycnidia* not seen.

TLC: no substances detected.

Ecology and distribution: *Peltigera koponenii* is primarily an epiphytic species growing on mossy trunks and branches in the montane (incl. on treefern trunks in deep valleys characterized by rare but acute frosts and irregular fires) and subalpine forests. It is also found overgrowing terrestrial mosses cushions in the subalpine zone, on gravel by rivers or streams and on artificial substrats, like hedges or garden fences in the montane forest zone. Its altitudinal range is 1850-4270 m.

Selected specimens examined (out of 46 collections): **Papua New Guinea: Central prov.**, Kosipe Swamp, Kosipe, 2000 m, November 1992, in swamp forest, *P. Lambley* 2028 (BM). **Eastern Highlands prov.**, Mt. Wilhelm slopes N of Lake Aunde, 11700 feet, June 1966, subalpine forest, terrestrial on fallen logs and decaying wood, *L. K. Wade* 8025 (COLO). **Madang prov.**, Huon Peninsula, Finisterre

range, Yupna valley, Teptep village, trail in NNW and deep valley in N direction, $5^{\circ}57'S$ $146^{\circ}33'E$, 2500 m, 30 July 1992, disturbed montane forest, gravel slopes along stream, *P. Diederich* 10968 (hb Diederich). **Northern prov.**, Owen Stanley Range, Myola surroundings of guest-house, $9^{\circ}09'S$ $147^{\circ}46'E$, 2100 m, 14-19 October 1995, small shrubs in grassland, disturbed by clearance, *E. Sérusiaux* s. n. (LG). Owen Stanley Range, Mt. Scratchley, c. 3500 m, 22 December 1985, *J. Ismay* 16957 (BM). **Southern Highlands prov.**, Mt. Giluwe, $6^{\circ}05'S$ $143^{\circ}50'E$, 3200 m, on thickly covered mossy ground in subalpine grasslands, 19 September 1984, *A. Bellamy* 1622 (B, CANB, H). **Simbu prov.**, Mt. Wilhelm, Pindaunde valley, near lake Piunde, $145^{\circ}03'E$ $5^{\circ}47'S$, 3600 m, 5-8 August 1992, on tree in subalpine forest, *A. Aptroot* 31346 (hb Aptroot). **West Sepik prov.**, S of Oksapmin, $5^{\circ}14'S$ $142^{\circ}12'E$, 1850 m, 6 January 1990, epiphyte on a tree in montane forest, *L. Hoffman* 90-103 (LG, hb Aptroot).

Notes: *Peltigera koponenii* is nearly identical with *P. canina* as it has a large thallus with tomentose upper surface, saddle-shaped apothecia growing on raised and rather large revolute lobes. However, its rhizines are typically fibrillose-coralloid (a feature sometimes seen in *P. canina*) and form dense 'bushy' masses that are never seen in *P. canina*. The lower surface of *P. koponenii* is thus very diagnostic. *Peltigera koponenii* clearly belongs to the monophyletic *P. canina*-group together with *P. praetextata*, *P. evansiana* and other undescribed species (Miadlikowska *et al.*, 2003); the entire group requires further studies. Quite interestingly, the ITS sequence of *P. koponenii* is virtually identical with that of *P. canina*, except for one substitution and one single nucleotide insertion in the former. A similar pattern characterizes *P. evansiana*, a species that is easily recognized by its laminal granular isidia, but is phylogenetically indistinguishable from *P. canina* based on ITS sequences. A further complementary argument to support the distinction of *P. koponenii* is that the genuine *P. canina* was not found among the numerous collections examined from Papua New Guinea.

Peltigera koponenii is easily distinguished from *P. fimbriata* by the absence of whitish hairs on the upper surface (this being a very typical feature of most populations of *P. fimbriata*), the absence of conspicuous marginal pycnidia, the fibrillose to coralloid rhizines and the septation and size of ascospores (5-7-septate and $65\text{--}80 \times 3.5\text{--}4 \mu\text{m}$ in *P. fimbriata* vs 3-septate and $44\text{--}53 \times 4\text{--}4.5 \mu\text{m}$ in *P. kopo-*

nenii). *Peltigera erioderma* is another related species with a usually large thallus and a tomentose upper surface and lack of secondary compounds. This species is, however, readily recognized by its horizontal apothecia, lack of conspicuous pycnidia and its much shorter hairs emerging from the tomentum.

Other species with fibrillose-coralloid or densely squarrose rhizines are:

- *P. fibrilloides* (Gyeln.) Vitik., known from the neotropical mountains (Vitikainen, 1998), may be a close relative of *P. praetextata* (Flörke ex Sommerf.) Zopf (similar veins patterns, frequent production of phyllidia, etc.) from which it differs by its fibrillose rhizines (rather long and slender, densely covered by short outspread lateral branches). Although somewhat reminiscent of those of *P. kopenhagenii*, the rhizines remain discrete and form a spongy cushion.

- *P. laciniata* (G. Merr. ex Riddle) Gyeln., a widespread species in the neotropical mountains (Vitikainen, 1998), is easily distinguished by its smaller thalli and lobes (usually not exceeding 0.5 cm wide near the extremities), the pale or almost white upper surface due to a dense tomentum, the occurrence of conspicuous, black, marginal pycnidia, and the production of zeorin. The rhizines are rather long, squarrosely branched and fasciculate and the veins tend to be covered by a thick layer (ca 0.2 mm) of coralloid dark hyphae; the lower surface of *P. laciniata* is thus quite characteristic.

- *P. retifoveata* Vitik., a disjunct circum-polar species of NW Europe (where it is very rare), N Asia and WN America (Goffinet, 1992; Vitikainen, 1994), can be distinguished by its large thallus, lower surface with a typical reticulate and foveate veining pattern and the production of depsides and terpenoids. Its rhizines are densely squarrose but are rather scattered and never form dense cushions as in *P. kopenhagenii*.

***Peltigera montis-wilhelmii* Sérus., Goffinet, Miądl. & Vitik. sp. nov.** (Figs 6 A-C)
Mycobank: 513030

Etymology: This new species is named after the mountain range where it was collected, the most famous Mt. Wilhelm range, probably the mountain most explored by botanists on the whole island.

A *Peltigera erioderma* differt thalli superna facie etomentosa.

Type: Papua New Guinea: Simbu prov., Mt. Wilhelm, Pindaunde valley, near the hut on the S-shore of lake Piunde, 145°03'E 5°47'S, c. 3600 m, 5 August 1992, subalpine forest remnants on W-slope of valley, *E. Sérusiaux* 13984 (LG—holotype).

Thalli +/- circular, 5-7 cm across, with imbricate rounded lobes to 4 mm wide, with a revolute or slightly raised margin. *Upper surface* smooth or rarely with some whitish pruina near the lobes margins, or minutely cracked near the margins, shiny, glabrous, usually with a nice orange-chamois to brownish colour, or pale greyish brown. *Lower surface* whitish to pale orange brown, darkening to almost black towards the center or in old parts, usually with the medulla hyphae easily seen under the dissecting microscope, with a distinct and well-developed network of rather large (0.2-0.5 mm), raised and densely anastomosing veins. *Rhizines* rather abundant, typically fasciculate, or sometimes simple to penicillate, pale when young but soon becoming black. *Apothecia* few but present on almost all thalli examined, typically horizontal, developed on swollen lateral lobes, disc reddish brown, remaining rather concave, ellipsoid, to 6.5 × 4 mm, margin typically incised crenate, and outer exciple rugose to verrucose and sometimes slightly tomentose or flocculose. *Ascospores* fusiform to acicular, with rounded ends, 3(-5)-septate, 50-61 × 4-5 μm. *Pycnidia* not seen.

TLC: no substances detected.

Ecology and distribution: *Peltigera montis-wilhelmii* seems to be rare and is currently known only from the Mt. Wilhelm area. It grows on branches in the upper montane forest zone and on the 'trunk' of treeferns in the subalpine forest, between 2800 and 3600 m elev.

Specimens examined: **Papua New Guinea:** **Simbu prov.**, same locality as the type, *E. Sérusiaux* 13987 (LG). *Ibid.*, c. 11 km on new road under construction from Gembogl to Goroka, 145°09'E 5°55'S, c. 2800 m, 9 August 1992, mossy montane forest, *E. Sérusiaux* s. n. (LG). *Ibid.*, Lake Aunde, 6 km SE of Mt. Wilhelm, 145°03'E 5°46'S, 3520 m, May 1966, on treefern stem in tussock grassland near field station, *D. McVean* 66236 (CANB, COLO).

Notes: *Peltigera montis-wilhelmii* is a very attractive species, characterized by its smooth, shiny and glabrous upper surface, large, rounded lobes with usually revolute

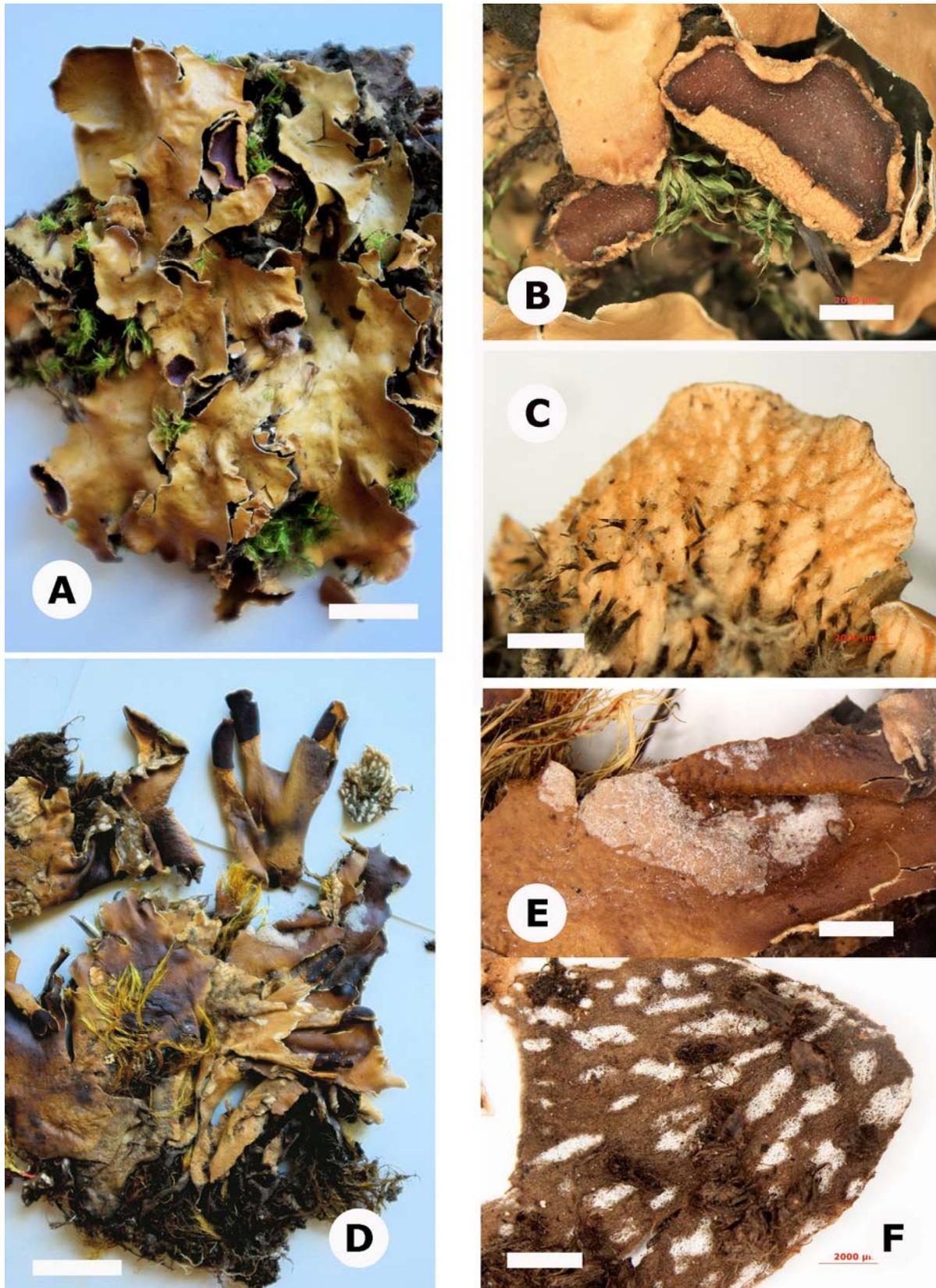


Fig. 6. A-C. *Peltigera montis-wilhelmii* (PNG, Mt Wilhelm, E. Sérusiaux 13984, LG—holotype). A. General habit. B. Apothecia. C. Lower surface at the edge of the lobes. D-F. *P. nana* (PNG, Mt Wilhelm, H. Sipman 35729, B). D. General habit. E. Incrustation on the upper surface. F. Lower surface. Scales: A, D = 1 cm, B-C, E-F = 2 mm.

margins, horizontal apothecia, mainly fasciculate rhizines growing on a distinct network of dark veins and lack of chemistry. The veins

and interstices pattern of the lower surface and the rhizines are strikingly similar to those of *P. papuana* and populations of the latter with a

smooth upper surface without pruina and with few, if any, marginal phyllidia are difficult to distinguish from *P. montis-wilhelmii*. In such cases the much larger lobes, the usually revolute margins, and especially the shiny upper surface are diagnostic. *P. montis-wilhelmii* is yet another glabrous species nested within the Sect. *Peltigera*, which is traditionally defined by the presence of laminal tomentum.

ITS sequences suggest that this species is most closely related to *P. erioderma*, a very similar species that differs, however, by its completely tomentose upper surface. Both species form a well-supported clade with ambiguous affinities within the Sect. *Peltigera*. The monophyly of *P. montis-wilhelmii* (MPIBS =100%; Fig. 2) is supported also by a unique pattern of the ITS1-HR shared by all specimens included in this study.

Peltigera nana Vain., Philippine Journal of Science, C. Botany, 8(2): 114, 1913

(Figs 6 D-F)

Type: The Philippines, Luzon, subprov. Lepanto, mons Malaya “*F. R. Bona 156*”, “*ad terram arenosam*” (TUR-V 9850 !; lectotype here selected).

= *Peltigera nana* var. *philippina* Gyeln., Ann. Mus. Nat. Hungar. 30 (pars Bot.): 133, 1936. *Nomen superfl.* **Syn. nov.**

Type: same as the lectotype.

= *Peltigera tereziana* var. *philippinensis* Gyeln., Ann. Mus. Nat. Hungar. 30 (pars Bot.): 133, 1936. **Syn. nov.**

Type: The Philippines, Luzon, subprov. Benguet, “*Bur. Sci. 5878 Ramos*”, “*ad terram arenosam*” (TUR-V 9855 — holotype !).

= *Peltigera macra* Vain., Philippine Journal of Science, C. Botany, 8(2): 114, 1913. **Syn. nov.**

Type: The Philippines, Luzon, prov. Pangasinan, “*Bur. Sci. 8298, Ramos*”, “*ad terram calcaream et argillaceam et humosam*” (TUR-V 9854 !; lectotype here selected).

Thalli not forming large rosettes but nevertheless quite robust, composed of imbricate lobes, not exceeding 0.5 cm in width, with a slightly upturned margin. *Upper surface* orange brown to dark brown, or greenish brown, almost blackish in old thalli, glabrous, smooth and shiny, usually with a distinct whitish pruina near the lobes margins and with large, incrustated patches towards the centre of the thalli, these patches appearing irregular and

slightly swollen when well developed. *Lower surface* pale orange to brown at the margins, soon becoming black (especially in old specimens), without veins but with elliptical and whitish to white interstices (in old specimens the white interstices are larger and hence the veins form a conspicuous network), surface hyphae of veins and especially interstices typically very distinct. *Rhizines* sparse, blackish, fasciculate or more rarely simple. *Apothecia* present, rather abundant, developed on digitated and raised lobes with revolute margins, to 1.2-1.5 mm long (incl. the apothecial disc); disc dark reddish brown, elliptical, 0.6-0.7 × c. 0.4 cm, saddle-shaped with a slightly incised or indistinct margin. *Ascospores* fusiform to acicular, straight or slightly curved 3(-5) septate, 62-82 × 5-6 μm. *Pycnidia* not seen.

TLC: tenuiorin, methylglyphosphate, glyphoric acid, peltidactylin and dolichorhizin (abundant), sometimes zeorin and other unidentified terpenoids.

Ecology and distribution: *Peltigera nana* has a wide ecological amplitude as it has been found on roadbanks and rocky outcrops, in rather open and secondary vegetation, at 1300-1800 m (lower montane forest zone), as well as on Mt. Wilhelm and in the mountains of the Huon Peninsula, on mossy and gravel soil, in the subalpine zone at 3500-3700 m elev. We have seen material of *Peltigera nana* from Luzon Island in The Philippines and Papua New Guinea; the species is mentioned from India (Himalaya) by Awasthi and Joshi (1982: 55) and is likely to be widespread in S-E Asia.

Selected specimens examined (out of 21 collections): **Papua New Guinea: Madang prov.**, S side of Ramu valley, Bundi village, along road to Bundi Gap, 5°44,9'S 145°14,1'E, 1300 m, 9 November 1995, on roadbank among secondary vegetation, *E. Sérusiaux* s. n. (LG). **Morobe prov.**, Mt. Sarawaket Southern Range, 2.5 km S of Lake Gwam and E of Mt. Enggum, 147°07'E 6°21'S, 3500-3570 m, 9 July 1981, deep S-sloping valley with scattered scrub and spring, on basic cliff, *T. Koponen* 32766 (H). Aseki-Menyamya Rd, Spreader Divide, 12 km NW of Aseki, 146°06' E 7°16'S, 1980 m, exposed, cleared area through montane forest, 21 January 1981, on shaded road cutting, *H. Streimann* 12057, 12098 & *E. Tamba* (CANB). Ogeranang, 1800 m, 28 June 1986, on roadside bank (partly sheltered), *P. W. Lambley* 17685 (BM). **Simbu prov.**, Mt. Wilhelm, Pindaunde valley, near the hut on the S-shore of lake Piunde, 145°03'E 5°47'S, c. 3600 m, subalpine forest remnants on W-slope of valley, 6 August 1992, *E. Sérusiaux* 13981 (LG). **Western Highlands prov.**,

Baiyer River, upper Trauna valley, 1700 m, 18 April 1986, 1700 m, on rocky outcrops of ridgetop, *P. W. Lambley* 16955 (BM).

Examined specimens of Peltigera melanocoma (all in L): **Indonesia, Java:** n° 62 coll. Junegh., in m. Pangerango 3-5000' (lectotype — here designated); n° 60 coll. Jungh [two collections in different envelopes]; n° 61 coll. Jungh; n° 63 coll. Jungh [two collections in different envelopes]; sine numero coll. Jungh, in cacumine m Sëndoro [+ illisible notes]; sine numero coll. Jungh, April. Silva montis Pangerango 3-5000'. Prov. Preanger, in decliv. austral. montis Panperango, prope Tjibodas, in horto montano, regio nubium, alt. +/- 1420 m, 28 April 1894, V. *Schiffner* Iter Indicum 1893/94, n° 3290.

Notes: *Peltigera nana* is distinguished by its usually robust thalli, albeit not forming large colonies or rosettes, growing on the ground, its upper surface usually with pruina at the lobes margins and sometimes large and conspicuous incrustated patches, its dark lower surface with an attractive network of distinct elliptical, whitish interstices, and surface hyphae usually typically very distinct. It does produce terpenoids, with dolichorhizin in large quantities.

In our phylogenetic tree, *P. nana* falls within the Sect. *Polydactylon*, forming a well-supported clade with *P. sumatrana*, *P. oceanica*, and *P. weberi*. *Peltigera nana* is closely related to *P. oceanica* (easily distinguished by the absence of tenuiorin and methylgyrophorate) and *P. weberi* (easily distinguished by the presence of marginal soredia) but its exact position remains ambiguous. However, the two specimens for which ITS sequences were produced do not form a monophyletic group, and more data are thus needed to assess the variation of that species.

Besides its original description and further comments by Gyelnik (1936), *P. nana* has only been reported from New Zealand [Murray, 1960, as *P. dolichorhiza* var. *nana* (Vain.) Js. Murray, and Galloway, 2000]. The morphological data provided for those populations (« broadly rounded, thin, papery lobes » ; Galloway, 2000: 25, 2007, 2008) clearly point to a different species.

Typification with further notes: Three collections are mentioned in the protologue for *P. nana* and all have been examined (TUR-V !); as quoted by Gyelnik (1936: 132-133), they are small and poorly developed. Their chemistry is identical: tenuiorin, methylgyrophorate, gyrophoric acid, peltidactylin, dolichorrhizin (abun-

dant) and zeorin. The specimen TUR-V 9850 («*F. R. Bona 156*») is the best developed and is thus here selected as the lectotype for the epithet *nana*. Gyelnik (1936: 133) considered this collection to represent a new variety, e. g. *P. nana* var. *philippina* Gyeln.; following our lectotypification, this epithet becomes superfluous. The collection TUR-V 9855 (subprov. Benguet, *Bur. Sci. 5878 Ramos*) was considered as a new variety of *P. tereziana* (var. *philippinensis*) by Gyelnik (1936: 133). Although the material is scanty, it matches very well *P. nana* and we can thus reduce this variety into synonymy with it.

As for *Peltigera macra*, we examined the three collections that are mentioned in the protologue (TUR-V!). Vainio claims that it differs from *P. nana* (and from *P. didactyla*; as *P. spuria* in the protologue) by its rhizines: «nervis e rhizinis breviter crebreque tomentosus dignota». We see no differentiation in rhizines morphology. The chemistry of the syntypes of *P. macra* is similar to that of *P. nana* but differs in the presence of several further tripernoids; these chemical differences are not sufficient to recognize a different taxon. The specimen «*Ramos 8298*» bears annotations by Vainio and is therefore here selected as the lectotype.

The identity of *P. melanocoma* Mont. & Bosch (*Lichenes Javanici*: 6, 1857; also in Miquelon, Pl. Jungh. 4: 432, 1857) has also been examined. Nine collections were received from L. The original publication mentions “Hab. ad terram et truncos ins. Javae (m. Pangerango 3-5000'), Jungh.”; the specimen labelled “n 62. Java coll. Jungh. in m. Pangerango 3-5000'” is designated as the lectotype. As all other specimens, it is terricolous, forms well-developed thalli with subparallel lobes, crenate-crispy margins, scattered incrustations on the upper surface, dense and rather long rhizines, reticulate dark veins separated by ellipsoid, whitish and thus forming a strong contrast interstices, digitate and rather small apothecia, and it produces tenuiorin, methylgyrophorate, gyrophoric acid, peltidactylin and especially abundant dolichorhizin. *Peltigera melanocoma* may be closely related to *P. nana* and even be conspecific. However, the thalli of *P. melanocoma* are much larger and with subparallel lobes with a

crispy margin, and thereby reminiscent also of *P. oceanica*. Pending further research on material from Java, we decided to retain both taxa as distinct.

Peltigera oceanica Gyeln., Fedde Repertor. 29: 9, 1931. (Figs 7 A-C)

Type: Philippines, Luzon, Benguet prov., Baguio, March 1907, A. D. E. Elmer 8456 p.p. (W—holotype !)

= *Peltigera oceanica* f. *dealbata* Gyeln., Fedde Repertor. 29: 9, 1931. **Syn. nov.**

Type: Philippines, Luzon, Benguet prov., Baguio, March 1907, A. D. E. Elmer 8456 p.p. (W—holotype !)

= *Peltigera oceanica* f. *luzoni* Gyeln., Fedde Repertor. 29: 9, 1931. **Syn. nov.**

Type: Philippines, Luzon, Benguet prov., Baguio, March 1907, A. D. E. Elmer 8456 p.p. (W—holotype !)

Thallus forming nice rosettes, to 10 cm across, made of rather narrow lobes (2-3 x 0.4-0.6 cm) with a typically raised and crisped lateral margin, usually showing the border of the lower surface; margins sometimes +/- regularly incised. *Upper surface* glabrous, smooth and shiny in most parts but sometimes slightly pruinose at lobes margins, pale greenish brown to dark brown, rarely incrustated in old parts, or distinctly foveolate (seen in only one collection). *Phyllidia* or *lobules* usually absent, rarely developed on lateral margins (perhaps damaged and regenerating parts). *Lower surface* white to pale orange with numerous, raised, pale brown (near the margins) to almost black (towards the centre) veins, leaving a nice network of numerous, elliptical and pale to whitish interstices of variable size. *Rhizines* usually abundant, simple to fasciculate, rather long, dark brown to blackish, usually with paler to almost whitish tips. *Apothecia* present or absent, sometimes quite abundant, typically saddle-shaped, developed on strongly revolute lobes at the extremities and usually raised, 0.4-0.7 cm long (incl. apothecial disc); disc dark reddish brown with a slightly raised and incised margin. *Ascospores* 5-septate, acicular, straight, with rounded ends, 48-55 × 4-5 μm. *Pycnidia* not seen.

TLC: only terpenoids (dolichorhizin abundant, peltidactylin and zeorin usually present in lower amounts, other unidentified

terpenoids sometimes present); tenuiorin and methylgyrophorate always lacking.

Nomenclature: The type collection is representative of the populations studied and, although inappropriate (the distribution pattern of this species has nothing to do with oceans), the epithet can be used without hesitation.

Ecology and distribution: *Peltigera oceanica* typically grows on gravel or sandy soil, usually over rock boulders near streams; it has never been found on humus, peat, plants debris, or on trees. Its altitude range is between 1250 and 3300 m. Beside the type collections (incl. *forma*'s) on Luzon Island in the Philippines archipelago, it has been mentioned from the "Papuan Provinces" by Martínez *et al.* (2003: 307) on early results of the present study. It is likely to be found elsewhere in S-E Asia.

Selected specimens examined (out of 21 species):

Papua New Guinea: Morobe prov., Mt. Sarawaket Southern Range, 4 km SE of Lake Gwam, 147°09'E 6°21'S, 3300 m, 5 July 1981, open grassland ('kunai') with scattered treeferns, on basic cliff, *T. Koponen* 31965 (H, LG) & 31966 (H). **Northern prov.**, Owen Stanley Range, Myola, surroundings of guest-house, 9°09'S 147°46'E, 2100 m, 14-19 October 1995, on boulders along Iora creek in open-field, *E. Sérusiaux* s. n. (LG). **Southern Highlands prov.**, Onim Forestry Station, 14 km NNW of Ialibu, 143°59'E 6°09'S, 2280 m, 18 September 1983, montane forest beside river, on rock near river bank, *A. Bellamy* 1295 (B, CANB). **Western Highlands prov.**, Al River Valley, NW of Nondugl, 2000 m, 3 April 1953, on rocks slightly above water level, *R. D. Hoogland* 3209 (CANB, H).

Notes: Only three species produce terpenoids in the absence of tenuiorin and methylgyrophorate (Vitikianen, 1986): *P. dolichospora* (Lu) Vitik., a member of Sect. *Polydactylon* known from Nepal and China/Sichuan, *P. laciniata* (G. Merr. ex Riddle) Gyeln., a common neotropical tomentose species, and *P. oceanica* Gyeln., described from The Philippines. The collections from Papua New Guinea have been carefully compared with the type material of the latter and they appear conspecific. Besides the absence of tenuiorin and methylgyrophorate, *P. oceanica* is distinguished by its glabrous upper surface, lobes with a raised and crisped (mainly laterally) margins that are sometimes slightly pruinose or incrustated, and a nice network of conspicuous elliptical interstices on the lower surface. *Peltigera nana* is quite similar, except for the lateral margin that is very rarely raised

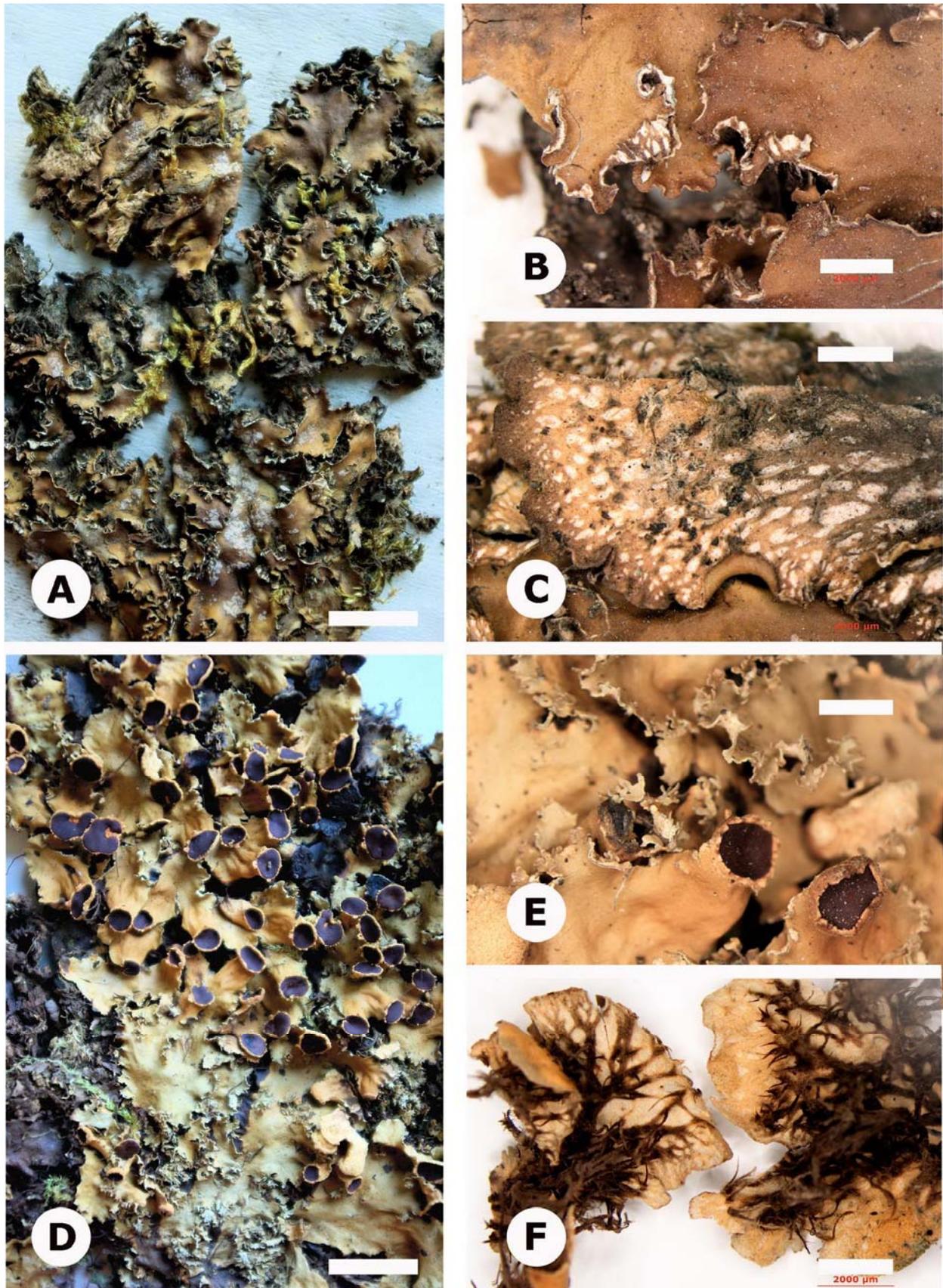


Fig. 7. A-C. *Peltigera oceanica* (PNG, Onim, A. Bellamy 1295, B). A. General habit. B. Crisped margins. C. Lower surface. D-F. *P. papuana* (PNG, Teptep, E. Sérusiaux 13656, LG—holotype). A. General habit. B. Apothecia and marginal phyllidia. C. Lower surface. Scales: A, D = 1 cm, B-C, E-F = 2 mm.

and crisped, and the production of tenuiorin and methylgyrophorate.

Peltigera oceanica falls within Sect. *Polydactylon*, forming a well-supported clade with *P. nana* and *P. weberi* (Fig. 1). Three representative samples from Papua New Guinea have identical ITS sequences that differ clearly in their hypervariable region from *P. nana* (MPIBS=91%). The relationships of these species remain ambiguous.

Peltigera papuana Sérus., Goffinet, Miądl. & Vitik. **sp. nov.** (Figs 7 D-F)

MycoBank: 513031

Etymology: Together with *P. fimbriata*, this species is the most distinctive taxon of the genus in Papua New Guinea, and is thus named after this country.

Ab aliis speciebus *Peltigerae* differt thalli superna facie laevigata vel scabrosa, marginibus phyllidiosis, elevatis et crenatis, et apotheciis horizontalibus.

Type: Papua New Guinea: Madang prov., Huon Peninsula, Finisterre range, Yupna valley, Teptep village, deep valley in N direction, 146°33'E 5°57'S, 2300-2750 m, 31 July 1992, mossy montane forest, *E. Sérusiaux* 13656 (LG—holotype).

Thallus forming attractive rounded rosettes to 10-12 cm in diam. in suitable conditions, lobes imbricate, not exceeding 0.5-0.7 cm wide, with raised and crenate (sometimes +/- crisped) margins (margins are distinctly revolute and swollen when an apothecium starts its development in them); lobes extremities sometimes with tufts of tiny whitish hairs. *Upper surface* orange brown, beige brown to grey brown, rarely bluish grey, smooth or faintly to distinctly scabrose with tiny pellucid hairs developing on the tiny 'verrucae', especially near the lobes margins, sometimes whitish-pruinose near young lobes extremities which therefore have a frosted appearance; some specimens with longitudinal cracks. Lateral margins frequently becoming incised-lacerate, with flattened, *branched lobules* that are usually fragile and easily removed; in well-developed specimens, lobules developing into typical, rather brittle *digitate phyllidia*, to 0.2 cm long, with their extremities sometimes tomentose or pruinose and distinctly enlarged. *Lower surface* whitish with the interwoven hyphae of the medulla and the bluish tinge of the photobiont easily seen under the dissecting microscope, with an attractive

network of 0.2-0.3 mm large and at least slightly raised veins, pale orange to brown near margin, otherwise dark brown to blackish, and separated by whitish elliptical interstices, especially near the margins. *Rhizines* abundant, rather long, dark brown to black, thread-like to penicillate, sometimes branched and rarely confluent. *Apothecia* usually present, numerous, typically horizontal, even at early stages, developed on swollen lateral, and occasionally tomentose lobes; disc dark reddish brown, remaining concave and partly covered by teared up and woolly remnants of vegetative tissues for quite a long time (thus giving them a crenate appearance), later becoming flat or irregular, rounded when mature to ellipsoid, reaching 6 × 4 mm but usually smaller; margins typically incised-crenulate and lobes carrying the disc usually distinctly tomentose. *Ascospores* fusiform and rather narrow, with +/- acute ends, 3-5-septate, (36-)38-51 × 4-5 μm. *Pycnidia* very rare, as small swollen brownish dots on the margins of lateral lobes; conidia not seen.

TLC: no substances detected.

Ecology and distribution: *Peltigera papuana* is a widespread species at mid elevations, found mainly on trees in primary to heavily disturbed montane forests; it is rather ubiquitous as it also grows on mossy soil and road banks. It has been found between 1700 and c. 2800 m, well below the subalpine zone. This is true only if we do not include two specimens of the "small form", collected at 3400 and 3600 m.

Selected specimens examined (out of 40 collections): **Papua New Guinea: Eastern Highlands prov.**, along jeep road from junction of Goroka-Kundaiawa main road toward summit of ridge on way to Marafunga, c. 5500 ft, 22 June 1968, forming dense pads up to one foot diam. over fern debris on trunks of *Pandanus*, *W.A. Weber & D. McVean*, Lichenes exsiccati distributed by the University of Colorado Museum, Boulder n° 319 (B, CANB, H, LG). Mt. Gahavisuka Provincial Park, 145°25' E 6°01'S, little disturbed mossy mountain forest, 2400 m, 3 August 1992, *P. Diederich* 10581 (hb Diederich). **Madang prov.**, Huon Peninsula, Finisterre range, Yupna valley, Teptep village, trail in NNW direction, towards Bambu Airfield, 146°33'E 5°57'S, c. 2500 m, 30 July 1992, on garden fence, *H. Sipman* 35270 (B). *Ibid.*, trail in N direction, 31 July 1992, on tree, *E. Sérusiaux* 13655 (LG). **Morobe prov.**, Mt. Sarawaket Southern Range, 4 km NNE of Lake Gwam, 147°9.5'E 6°19'S, 2850 m, 4 July 1981, open grassland with scattered treeferns, *T. Koponen* 31592 (H). **Simbu prov.**, Mt. Wilhelm area, c.

11 km on new road under construction from Gembogl to Goroka, 145°09'E 5°55'S, c. 2800 m, 9 August 1992, road bank in mossy montane forest, *E. Sérusiaux* 14106 (LG). Kombugomambuno, 8 km SE of Mt. Wilhelm, 145°03'E 5°47'S, 3320 m, May 1967, epiphytic in subalpine tussock grassland with tree ferns, *L. K. Wade* (CANB; 2 collections). **Southern Highlands prov.**, Kengaput, Mendi-Kauga Road, 6 km SSE of Mendi, 6°12'S 143°4'E, 1700 m, 10 September 1982, on *Pandanus* stem in *Dacrydium* dominated swamp, *H. Streimann* 23694 (B). **Western Highlands prov.**, Nebilyer River, 28 km WNW of Mt. Hagen, 5°48'S 143°49'E, 2760 m, 23 June 1982, on upper branches of a small *Elaeocarpus* in disturbed montane forest, *Nothofagus*, Podocarpaceae and Cunoniaceae dominated, *H. Streimann* 20585 (B, CANB, H).

Examined specimens for the "small" form akin P. erioderma: Papua New Guinea: Northern Prov., Owen Stanley Range, Myola, c. 3 km NE of guest-house, 9°08'S 147°47'E, 2700 m, 16 October 1995, in treefern grassland in deep valley (frost hollow), *H. Sipman* 38336 (B). **Simbu prov.**, Mt. Wilhelm, Piunde valley, 3400 m, 13 April 1987, on treefern, *P. W. Lambley* 16965 (BM). **Western Highlands prov.**, N of summit of Mt. Giluwe, c. 3600 m, 31 August 1987, *P. W. Lambley* 16963 (BM).

Selected specimens of P. tereziana examined (out of 10 collections): **Australia**, New South Wales (NSW): Southern Tablelands. Bendoura Range: the hearts of 'Marble Arch', past 'The Big Hole', 33 km (direct) SSW of Braidwood. 35°43'30S 149°41'20E, 620m, limestone. Very moist/wet area with mosses, ferns (*Dicksonia* sp.) and elderberry bush (*Sambucus* sp.), foliose lichen on a large rock that was exposed from within the creek – downstream from the caves, January 1999, *T.K. Overeem* 11 (CANB). NSW: Southern Tablelands, Moodong Creek, Marble Arch, Deau, 34 km SW of Braidwood. 35°43'30"S 149°41'24"E 580m, dry sclerophyll on moderate slope to creek, on semi-shaded boulder in seasonal stream. 11 January 1999, *H. Streimann* 63484 (CANB). NSW: Poblue Swamp, Barrington Tops State Forest, 50 km WNW of Gloucester, 31°58'S 151°26'E 1450m, *eucalyptus pauciflora*, *Leptospermum* and epicridaceae fringed swampy area. On *Eucalyptus*, 25 April 1990, *J. A. Elix* 24690 (CANB). Victoria, Moranding, Kilmore, 144°57'E 37°18'S, April 1890, on rock by creek, *F. R. M. Wilson* 1188 (VIC-isotype). **New Zealand**, North Island, Hawke's Bay Land District, Puketitiri, 176°31'E 39°17'S, on soil, coll. between 1975 and 1985, *J. K. Bartlett* s. n. (CHR 449001). South Island, Otago Land District, Moa Creek, on soil, 17 February 1979, *I. Brown* s. n. (CHR 490548). *Ibid.*, Lammermoor Range, on soil, 21 March 2007, *D. J. Galloway* s. n. (LG).

Notes: Peltigera papuana is easily recognized by its smooth to scabrose upper surface, usually with pruina near lobes margins, small lobes with raised and crenate margins, presence of marginal phyllidia, horizontal apothecia developed on small lobes and absence of chemical compounds. Some

specimens, though well-developed, almost lack marginal phyllidia, and are morphologically similar to *P. montis-wilhelmii*, which differs by the larger and glabrous lobes with slightly raised to revolute margins and a shiny upper surface (see further comments under this species).

ITS sequences of representative collections show that *P. papuana* likely belongs to the *P. rufescens*-group (*sensu* Miadlikowska *et al.*, 2003) with close affinities to the newly described *P. granulosa*, and the South American *P. laciniata* (Fig. 2). Support for the monophyly of this taxon is lacking.

Whether these populations should be assigned to *P. tereziana* Gyeln. (Öst. Bot. Z. 77: 220, 1928; = *P. subhorizontalis* Gyeln., Ann. Cryptog. Exot. 5: 39, 1932; Vitikainen, 2004) has been carefully assessed. Indeed, the type material of the latter is described by Galloway (1985: 365-366; 2000: 40-41) as forming 'neat rosettes', with lobes 'glossy in parts, rarely delicately white-pruinose in parts imparting a slightly frosted appearance to lobes, margins incised-lacerate or minutely crenate-lobulate', with horizontal apothecia and lacking terpenoids or depsides. Examination of type material and other specimens from Australia and New Zealand (see list below) shows it is a different species. The surface is never scabrose and is usually smooth and glossy, with distinctly pruinose and frosted patches, usually at the margins but sometimes covering large parts of the surface. The lobes are sometimes incised and lobulate but never form the typical brittle digitate phyllidia typical of the Papuan specimens. Furthermore *P. tereziana* is primarily terricolous rather than epiphytic. A further, more subtle difference pertains to the horizontal position of apothecia: in *P. papuana*, they immediately develop in a horizontal position with a slightly concave and crenate disc, whereas in *P. tereziana*, they develop in an erect position with a slightly saddle-shaped disc, and they eventually get laterally larger and adopt a horizontal position. Furthermore, inferences from ITS sequences obtained from typical collections of *P. tereziana* reveal that this species shares a common ancestry with *P. membranacea* and *P. degenii* (Fig. 2) and not with members of the *P. rufescens*-group, which

includes *P. papuana*. *Peltigera tereziana* is thus yet another species of Sect. *Peltigera* lacking tomentum.

In Papua New Guinea, three specimens were first assigned to a small form of *P. erioderma* as they share its diagnostic characters: tomentose upper surface, horizontal apothecia and lack of chemical compounds. However, they form much smaller rosettes (to 3-6 cm in diam.) with imbricate lobes c. 0.5-0.7 cm wide, and are akin to *P. papuana* in general habit. Indeed, ITS sequences from one of these collections (*H. Sipman* 38336, *P. papuana* 7 in Fig. 2) reveal affinities to specimens typical of *P. papuana* even though they lack some diagnostic characters of this species, especially the smooth to scabrose upper surface and the production of marginal phyllidia. However, none of the characters of these specimens are *a priori* incongruent with *P. papuana*. No further sequences could be obtained and we thus refrain from distinguishing another taxon on that basis.

Peltigera sumatrana Gyeln., Rev. Bryol. Lichénol. 5: 72, 1932. (Figs 8 A-C)

Type: Indonesia, Sumatra, Korinchi Peak, 7300', 28 April 1914, *H. C. Robinson & C. B. Kloss* n° 139 (W—holotype !)

Species forming large (to 10 cm across) and rather robust *thalli*, with large, rounded lobes to 1 cm wide, or smaller ones with more narrow or elongate lobes not exceeding 0.5-0.7 cm wide; margin revolute. *Upper surface* glabrous, smooth and shiny in most parts but sometimes distinctly pruinose at lobes margins or on lateral phyllidia or lobules (when developed), pale beige brown, bluish grey or dark brown. *Phyllidia* or *lobules* usually absent, sometimes developed on lateral lobes, margins or rarely the surface of damaged and regenerating parts of *thalli*, to 2-3 mm in length, some typically pruinose. *Lower surface* pale brown or orange with a reddish-brown to black araneous cover near the margins, but soon becoming jet black, usually without any veins but with elliptical and whitish interstices towards the center. *Rhizines* usually abundant, typically fasciculate and densely branched, sometimes forming a dense cushion on the lower surface or remaining well separated from each other and arranged in concentric rows.

Apothecia present or absent, sometimes quite abundant, developed on strongly revolute lobes at the extremities which are not necessarily raised, 0.5-0.8 cm long (incl. apothecial disc), typically saddle-shaped; disc dark-reddish brown with a slightly raised and incised margin. *Ascospores* acicular to fusiform, straight or slightly curved, 3-5-septate, with rounded ends, 58-78 x 4-5 µm.

TLC: tenuiorin, methylglyphosphate and terpenoids; the full spectrum includes 9 terpenoids, but dolichorhizin always dominant and peltidactylin and zeorin always present but in smaller quantities.

Nomenclature: The holotype has been examined, including by TLC: although quite small and badly preserved, the specimen is clearly conspecific with the numerous populations from Papua New Guinea, that are thus treated as *P. sumatrana*.

Ecology and distribution: *Peltigera sumatrana* is typically a species of the montane forest (1850-2900 m), where it can be quite common on trees, over terricolous mosses and even on peat (e. g. Gahavisuka Provincial Park, Eastern Highlands prov.). A slightly different population has been sampled at lower elevation (1300-1600 m, see below). This species reaches the alpine zone around 3600-4000 m where it grows in rather protected niches, and never on bare soil and gravel. It has also been found on 'artificial' substrates in the montane forest zone, like rocky road banks, soil in gardens, or even on the roof of huts. Beside the type collection from Sumatra, it has never been mentioned in the literature. It is most likely widespread in the mountains of S-E Asia, and is new for New Guinea.

Selected specimens examined (out of 42 collections): **Papua New Guinea: Eastern Highlands prov.**, Mt. Gahavisuka Provincial Park, 11 km N of Goroka, along trail to lookout, 6°1'S 145°25'E, 2400 m, 3 August 1992, little disturbed mossy montane forest, *P. Diederich* 10585 (hb Diederich). *Ibid.*, 5 November 1995, little disturbed mossy mountain forest, dominated by *Castanopsis*, *E. Sérusiaux* s. n. (LG). **Madang prov.**, Huon Peninsula, Finisterre range, Yupna valley, Teptep village, trail in NNW direction towards Bambu Airfield, 146°33'E 5°57'S, c. 2300-2650 m, 30 July 1992, disturbed montane forest, with scattered old trees and regenerating shrub layer after fire, *E. Sérusiaux* 13609 (LG). **Morobe prov.**, Mt. Kaindi, 5 km W of Wau, 7°19'S 146°44'E, 2300 m, 26 July 1982, on base of small *Evodiella* in disturbed *Nothofagus* forest near summit, *H. Streimann* 22425 (B, CANB). Saruwaged

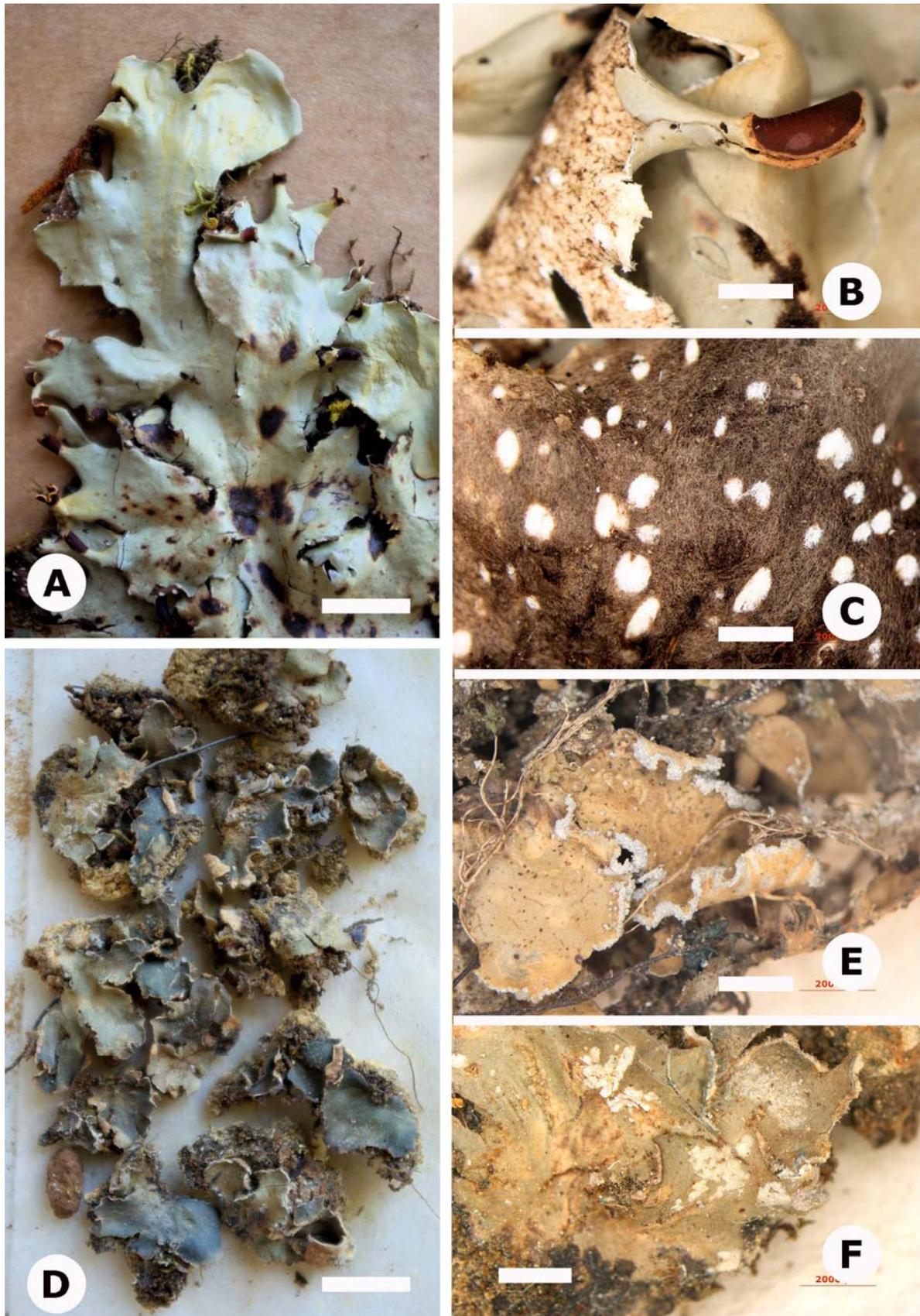


Fig. 8. A-C. *Peltigera sumatrana* (PNG, Gahavisuka, 5 November 1995, E. Sérusiaux s. n., LG). A. General habit. B. Apothecia and margin of the lower surface. C. Lower surface. D-F. *P. weberi*. D, F (PNG, Goroka, W. A. Weber and D. McVean L-50140, COLO—holotype). E. (PNG, Mt Kaindi, H. Streimann 33372, CANB). D. General habit. E. Sorediate margins. F. Incrustations on the upper surface. Scales: A, D = 1 cm, B-C, E-F = 2 mm.

Range, Honzeukngon village S of Derim in Timbe valley, 147°06'E 6°13'S, 1850 m, 7-8 March 1987, on branches and small trunks in clearing, *H. Sipman* 24513 (B). **Simbu prov.**, Mt. Wilhelm, Pindaunde valley, near the hut on the S-shore of lake Piunde, 145°03'E 5°47'S, 3600 m, 5 August 1992, subalpine forest remnants on W-slope of valley, *E. Sérusiaux* 13985 (LG). **Southern Highlands prov.**, Onim Forestry Station, 14 km NNW of Ialibu, 6°09'S 143°59'E, 2250 m, 15 September 1982, cleaned areas with grasses between road and the river, *H. Streimann* 24783 (B, H, LG). **Western Highlands prov.**, Jimi-Waghi Divide, 9 km N of Banz, on Tabibuga road, 5°43'S 144°38'E, 2400 m, 7 July 1982, on treelet stem, *H. Streimann* 22295 (H). **Indonesia, Irian Jaya:** Carstenz Mts, Carstenz meadow, 3540 m, 10 December 1971, open tussock grassland with *Astelia* hummocks, on peat, *G. Hope* CGE L3 & L6 p.p. (CANB).

Notes: Inferences from substitutions in the ITS sequences reveal that this species is related to the *P. oceanica*-complex and thus falls into Clade 1 within the Sect. *Polydactylon*. The accession *P. sumatrana* 5, although morphologically similar to the remaining specimens of *P. sumatrana* has a different ITS1-HR pattern; although it is placed outside of the *P. sumatrana*-clade (MPIBS=96%; Fig. 1), we retain it within that species pending further studies.

Peltigera sumatrana is easily distinguished by its usually large thalli with a smooth upper surface, lower surface without veins, most usually jet black but with elliptical and whitish interstices, fasciculate and densely branched rhizines, saddle-shaped apothecia and production of terpenoids dominated by dolichorhizin. Populations growing on bare ground by roads or in gardens can be atypical as they are composed of smaller individuals with smaller lobes; they can be easily identified by their chemistry and by the typical lower surface, especially the fasciculate and densely branched rhizines.

Populations here referred to the same species have been extensively sampled in Bundi, in a lower montane forest (c. 1300-1600 m) on the southern side of the Ramu river. They match *P. sumatrana* in all morphological details (including the occurrence of pruina on young lobes, and sometimes phyllidia on lateral lobes, lower surface and rhizines, and size and septation of ascospores) except for two features: they form less robust and even fragile, sometimes very thin thalli with a +/- foveate surface — thus reminiscent of *P.*

dolichorhiza — and most examined thalli (4 out of 5) fail to produce zeorin. Compared to the usually quite robust specimens of typical *P. sumatrana* that were all collected at higher elevations, they look quite different and may represent distinct populations evolving towards such a status. The ITS sequence of a representative specimen (*P. sumatrana* 4, Fig. 1) is identical to that of some more robust and hence typical specimens *P. sumatrana*.

Specimens examined: **Papua New Guinea: Madang prov.**, S side of Ramu valley, Bundi village, on slope towards Mt. Pizetara, 5°44.9' S 145° 14.1'E, 1300-1600 m, 8 November 1995, disturbed montane forest, *E. Sérusiaux* 16401 & 16402 (LG), *H. Sipman* 39212 & 39213 (B).

Peltigera ulcerata Müll. Arg., *Flora* 63: 261, 1880.

Type: "Prope Apiahy Brasiliae merid. crescit: Puiggari n. 1023 p. p." (G—holotype !; W—isotype !).

Thallus usually quite small and inconspicuous, especially when growing amongst healthy pleurocarpous mosses on trees, but sometimes reaching 5-6 cm in diam. when being a pioneer species on its substrate, formed of adjacent or imbricate lobes, mostly suborbicular but sometimes elongate, 0.5-1.0 cm wide, typically concave (especially when young), with a +/- revolute margin. *Upper surface* glabrous, smooth, rarely +/- scabrose, dull or slightly shiny. *Soralia* always present, orbicular to ellipsoid, c. 1-2 × 1 mm, laminal but most usually near the lobes margins and becoming +/- marginal in old specimens, sometimes confluent; when young with a distinct rim of remnants of cortex. *Soredia* usually bluish-grey, farinose to granular, abundant or almost absent. *Lower surface* pale orange to greyish, with a network of slightly raised, greyish dark veins that are inconspicuous near the margins. *Rhizines* simple to fasciculate, usually abundant, dark brown except near the margins where they are much paler (especially at their base). *Apothecia* and *pycnidia* not seen.

TLC: methylgyrophorate in soralia (which thus react C⁺ red); gyrophoric acid detected in some but not all collections.

Nomenclature: The use of this epithet has been soundly established for a long period and no problem was detected.

Ecology and distribution: *Peltigera ulcerata* is mainly a muscicolous species on trees in montane forests, including in disturbed localities, but it can also grow on dead logs on the ground, on mosses over rocks and amongst terricolous mosses in alpine vegetation. It has not been collected on roadbanks or on ground near streams or rivers. Its altitudinal range extends from 2300 to 4200 m. This species is widespread in the tropical mountains of the three continents and in temperate areas of the southern hemisphere (Swinscow and Krog, 1988: 203; Galloway, 2000: 41-42; Goffinet *et al.*, 2003), and occurs also in the Western Himalayan Province (Martínez *et al.* 2003: 307). Aptroot and Sipman (1991: 232) reported the first collections from Papua New Guinea.

Selected specimens examined (out of 13 collections): **Papua New Guinea: Eastern Highlands prov.**, Mt. Gahavisuka Provincial Park, 11 km N of Goroka, 6°01'S 145°25'E, c. 2300 m, 5 November 1995, little disturbed mossy montane forest dominated by *Castanopsis*, 5 November 1995, *E. Sérusiaux* 16200 (LG). **Madang prov.**, Huon Peninsula, Finisterre range, Yupna valley, Teptep village, 146°33'E 5°57'S, 2300 m, 30-31 July 1992, on hedges of *Cordyline* between gardens, *A. Aptroot* 32278 (hb Aptroot). **Northern prov.**, Owen Stanley Range, Myola, surroundings of guest house, 9°09'S 147°46'E, 2100 m, 14-19 October 1995, in primary forest in valley, *E. Sérusiaux* s. n. (LG). **Southern Highlands prov.**, 30 km after Kaupena, 6°12'S 143°55'E, 2350 m, 11 October 1989, rainforest clearfelling area, on dead wood, *K. Van der Gucht* 89-695 (hb Aptroot). **Simbu prov.**, Mt. Wilhelm, Pindaunde valley, along track to the summit, 145°03'E 5°47'S, 4200 m, 7 August 1992, on soil in alpine vegetation, *A. Aptroot* 31572 (hb Aptroot).

Notes: *Peltigera ulcerata* belongs to the *P. didactyla*-complex (Goffinet *et al.*, 2003). It is diagnosed by its small, orbicular to elongate lobes with a smooth, mostly shiny brown upper surface and elliptical, laminal to submarginal or marginal soralia producing rather farinose and usually bluish soredia. Some small and sterile specimens of *P. didactyla* may be difficult to distinguish when their upper surface has almost no tomentum; they can be recognized by their mostly laminal soralia and coarser, partly corticate soredia.

Based on its ITS sequence a representative collection from Papua New Guinea is resolved as sister to a specimen of *P. ulcerata* from Rwanda (Fig. 2), corroborating its identification, and hence the presence of this taxon in Papua New Guinea.

***Peltigera weberi* Sérus., Goffinet, Miądl. & Vitik. sp. nov.** (Figs 8 D-F)

Mycobank: 513032

Etymology: This new species is named after Prof. W.A. Weber (University of Colorado) who was the first lichenologist to collect lichens extensively in Papua New Guinea; he brought splendid specimens from the upper montane zone of Mt. Wilhelm and several became types of new species, such as *Calathaspis devexa* I.M. Lamb & W.A. Weber, *Dimerella weberi* Vězda and *Pertusaria gyalectoides* Vězda.

Ab aliis speciebus *Peltigerae* differt thalli superna facie etomentosa, marginis farinoso-sorediosis et terpenoideas continente.

Type: Papua New Guinea: Eastern Highlands prov., road just above Goroka on way to power plant, 4000 feet, 22 June 1968, on clay banks beside the road, *W. A. Weber & D. McVean* L-50410 (COLO—holotype; LG—isotype).

Thallus small and inconspicuous, made of rounded, isolated or imbricated lobes, mostly c. 0.5 cm large near the extremities, pale olive brown to dark bluish green, flat or slightly concave, with the margins typically upturned when sorediate. *Upper surface* glabrous, smooth, rarely somewhat scabrose, and rather dull. *Soralia* always present but not developed on all lobes, typically marginal and hardly spreading on the lower surface; soredia usually bluish-grey, farinose to granular. *Lower surface* orange to greyish, with a poorly developed network of slightly raised, greyish veins, which can be hardly visible at the margins. *Rhizines* simple to fasciculate, not abundant, pale brown. *Apothecia* and *pycnidia* not seen.

TLC: tenuiorin, methylgyrophorate, dolichorhizin and zeorin.

Ecology and distribution: *Peltigera weberi* is a rare species and grows on earth and rock debris, and on road banks, between 1200 and 1450 m.

Specimens examined: **Papua New Guinea: Madang prov.**, S side of Ramu valley, Bundi village, along road to Bundi Gap, 5°44.9'S 145°14.1'E, 1300 m, 9 November 1995, on roadbank among secondary vegetation, *H. Sipman* 39314 (B). **Morobe prov.**, Mt. Kaindi road, 5 km WNW of Wau, 146°41'E, 1450 m, 9 January 1983, montane forest on moderate slope, on the ground and on rock, *H. Streimann* 33372 (CANB).

Notes: *Peltigera weberi* is easily distinguished by the following combination of characters: inconspicuous glabrous and smooth thallus, soralia present and strictly marginal

and production of terpenoids. *Peltigera cichoracea* (Sect. *Horizontales*) produces soredia and terpenoids but typically forms large thalli (10 cm in diameter) on trees. All other sorediose species found in Papua New Guinea differ by their lack of terpenoids; moreover *P. didactyla*, *P. extenuata* and *P. ulcerata* (Sect. *Peltigera*) differ by their predominantly laminal soralia, whereas *P. granulosa* (also Sect. *Peltigera*) has a granulose margin that is never genuinely sorediose. *Peltigera didactyla* and *P. extenuata* differ further by their tomentose upper surface. The allotatric *P. collina* (Sect. *Horizontales*) has glabrous lobes with marginal soralia, too, but these are coarsely granular, partly corticate and finger-like and thus easily distinguish this species from *P. weberi*.

The ITS sequence of a single representative collection demonstrates that *P. weberi* belongs to Sect. *Polydactylon* and is closely related to *P. oceanica* and *P. nana* (Fig. 1). Currently this is the only sorediate species in the Sect. *Polydactylon*.

Lichenicolous fungi

Although lichenicolous fungi are not the main purpose of this study, we report here species growing on *Peltigera* thalli from Papua New Guinea. We confirm the existing records of the following peltigericolous taxa from Papua New Guinea (Aptroot *et al.*, 1997: 81, 97, 112 & 208): *Leptosphaerulina peltigerae* (Fuckel) Riedl, *Lichenopeltella peltigericola* (D. Hawksw.) R. Sant., *Nectriopsis lecanodes* (Ces.) Diederich & Schroers and *Vezdaea dawsoniae* Döbberler. During this study, three additional species were found (identifications by Dr. P. Diederich): *Corticifraga fuckelii* (Rehm) D. Hawksw. & R. Sant., on unidentifiable necrotic material (Northern prov., Owen Stanley Range, Myola, 9°08'S 147°47'E, 2700 m, 16 October 1995, on tree fern, *E. Sérusiaux* s.n., LG); *Corticifraga peltigerae* (Fuckel) D. Hawksw. & R. Sant., on *P. kopenhagenii* (Simbu prov., Mt. Wilhelm, 4270 m, 26 August 1970, *L. Stapf* s. n., CANB); *Scutula epiblastematica* (Wallr.) Rehm, on *P. kopenhagenii* (Central prov., Kosipe Swamp, 2000 m, November 1992, *P. W. Lambley* 2028, BM).

Acknowledgments

The authors are very grateful to the curators of the following herbaria who placed interesting specimens at their disposal: B, BM, CANB, CHR, COLO, L, U, and to their colleagues and friends who also made large collections available, especially Dr. André Aptroot, Paul Diederich, Peter Lambley and Harrie Sipman. A set of specimens from East Africa (Kenya and Rwanda) was kindly made available to us by Prof. Dr. Eberhard Fischer and Dr. Dorothee Killmann. A preliminary work by Florin Crisan (Univ. 'Babes-Bolyai', Cluj-Napoca, Roumania) on the material collected by E. Sérusiaux has been helpful for the comprehension of the variation of several widespread species. They also want to thank very warmly Mr. I. Cremasco (University of Liège) for his precious help in performing TLC analyses, Dr. P. Diederich (National Museum of Natural History in Luxemburg) for his help in the identification of lichenicolous fungi, Prof. Jack A. Elix (Australian National University in Canberra) for TLC and HPLC examination of *Peltigera dolichorhiza* s. lat. C, Dr. David J. Galloway and Dr. Simone Louwhoff for kindly providing specimens of *P. tereziana* from New Zealand and Australia, and Dr. Robynn Shannon for leading the initial sequencing effort. The work by Emmanuël Sérusiaux was made under several awards from the Belgian "Fonds de la Recherche Fondamentale Collective" that funded his expeditions to Papua New Guinea and his visit to the University of Connecticut. His stay in Helsinki was supported by the EU (European Union) Large Scale Facility Program. Bernard Goffinet acknowledges support from the University of Connecticut.

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