The Lichenologist **42**(5): 563–585 (2010)
doi:10.1017/S0024282910000083

Psorophorus and *Xanthopsoroma*, two new genera for yellow-green, corticolous and squamulose lichen species, previously in *Psoroma*

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Abstract: *Psoroma microlepideum* is reduced to a synonym of *P. fuegiense*. The species differs in several characters from *P. pholidotum*, and it overlaps geographically with the latter, which is neotypified here. These two species are now placed in the new southern South American genus *Psorophorus*, differing from *Psoroma* s. str. in being corticolous, having adpressed squamules on a distinct, dark prothallus, lacking melanins, having a thin cortical layer and a simpler IKI+ apical ascus structure. Two other widespread, panaustral species are the only ones in *Pannariacae* containing usnic acid. The primarily fertile species has been known as *Psoroma pholidotoides*, but the type contains pannarin rather than usnic acid, and the correct name for the primarily fertile taxon with usnic acid is *Psoroma contextum* Stirt. This is together with *P. soccatum* R. Br. ex Crombie is now placed in the new genus *Xanthopsoroma*. In addition to usnic acid, both species have a series of distinct terpenoids, some in major quantities. Like *Psorophorus*, they are corticolous, but have long, more or less nodulose, apical perispore extensions, and an IKI+ apical ascus tube structure which is longer and thinner, including a diffuse tholus reaction, and often an external apical sheet. Phylogenetically, these two genera are shown to be monophyletic and different from *Psoroma* s. str. based on an analysis of ITS and nrLSU rDNA. This analysis also shows that among the ten species focused on in this study, nine species (two in *Xanthopsoroma*, two in *Psorophorus* and five in *Psoroma* s. str.) are monophyletic, based on two to six sequences of each species. *Psoroma hypnorum* remains polyphyletic. All names now belonging in *Psorophorus* and *Xanthopsoroma* are typified.

Key words: austral, lichens, new species, *Pannariaceae*, phylogeny

Introduction

The genus *Psoroma* Michx. is defined by its generitype *P. hypnorum* (Vahl) S. F. Gray, which is a tripartite species, brown from melanins and without any TLC-detectable compounds. It is primarily terrestrial, and most often grows on a bryophyte cover, but can sometimes grow on trunks, particularly on the decomposing bases or fallen logs. Its asci have a characteristic apical ascus structure stained blue by IKI and referred to as a manubrium, and its ellipsoid proper spores are surrounded by strongly verrucose perispores (see illustrations in Jørgensen 1978). Its amyloid structure has later been referred to as an 'apical ring-structure' (Jørgensen 2001). About 15 primarily terricolous species share most of these characteristics and belong to the *P. hypnorum* group. There is no monograph on these species and some related corticolous species have uncertain generic affiliations. All the species are austral, but in addition to *P. hypnorum* the following three species have also reached the Northern Hemisphere: *P. tenue* Henssen (Jørgensen 2004), *P. cinnamomeum* Malme (Jørgensen 2001), and *P. paleaceum* (Fr.) Timdal & Tønsberg (Timdal & Tønsberg 2006).

Until a decade ago, *Psoroma* was a collective name for all tripartite *Pannariaceae* species with thalline excipuli. However, most

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foliose species have now been placed in *Pannaria* (Ekman & Jørgensen 2002; Elvebakk & Galloway 2003; Passo & Calvelo 2006; Passo *et al*. 2008). Among the remaining squamulose and primarily corticolous species, Elvebakk & Bjerke (2005) transferred *Psoroma isabellinum* Vain. to *Pannaria*, although they believed it merits a position within an as yet undescribed genus. Its position in *Pannaria* was maintained by Passo *et al*. (2008), who also transferred *Psoroma implexum* Stirt. to *Pannaria*. They also included *Pannaria hispidula* (Nyl.), a species mostly treated as a *Psoroma*, in *Pannaria*.

Ekman & Jørgensen (2002) showed two distinct *Pannaria* and *Psoroma* clades in their phylogenetic trees. This was confirmed by Passo *et al*. (2008) with a much better selection of taxa. They treated the two usnic acid species, *Psoroma pholidotoides* (Nyl.) Trev. and *P. soccatum* R. Br. ex Crombie, in a separate clade, and included three corticolous species (*P. pholidotum* (Mont.) Müll. Arg., *P. fuegiense* (Zahlbr.) Henssen & P.M. Jørg., and *P. aphthosum* Vain.) in their *Psoroma* clade.

At present the *Psoroma* clade is monophyletic, based on the analysis of a limited number of sequences. However, it is an assemblage of species with no clear set of shared characters. Its apical amyloid ascus structure separates it clearly from neighbouring *Pannaria* species, but is rather similar to structures in other species in the *Pannariaceae* (see illustrations by Keuck 1977) with visual patterns also depending on the IKI concentrations applied. Its photobiont pattern is now shared with many species within *Pannaria* s. lat., and the *Psoroma* clade also includes the cyanospecies *Santessoniella polychidioides* (Zahlbr.) Henssen (Ekman & Jørgensen 2002; Passo *et al*. 2008). The genus *Psoroma* is still heterogeneous, with a large variation in thallus morphology including paleotropical foliose species, with subgroups which are primarily either terricolous or corticolous and with considerable variation in chemistry, whereas important characters such as perispore and amyloid ascus structures have not yet been sufficiently studied. In view of this situation, we have attempted to find monophyletic entities within this group, which can be characterized by better defined synapomorphies than those valid for *Psoroma* as defined by its present members.

This objective is in close agreement with views expressed by Jørgensen (2003), who listed 38 accepted *Psoroma* species in his review of *Pannariaceae*, although seven of these have later been transferred to other genera. He accepted only "*c*. 20" species within the *Psoroma hypnorum* group (an earlier estimate of "$\approx$15" was indicated by Ekman & Jørgensen 2002) as part of the genus, whereas the remaining ones "must be placed in appropriate genera eventually".

In addition to their uncertain generic affiliations, many *Psoroma* species also remain poorly understood, as critical characters such as chemistry, perispore structure and internal ascus structures normally were not included in the original descriptions. As a contribution to an increased understanding of this group of lichens, the present study addresses species' definitions and the generic positions of two complexes at present retained within *Psoroma*. Among the corticolous and squamulose *Psoroma* species, *P. pholidotum* (Mont.) Müll. Arg. has the earliest basionym (Montagne 1835, as *Parmelia pholidota* Mont). It was described from the Chilean Juan Fernández Islands, but has been interpreted from various other areas. When *Psoroma microlepideum* Malme from southern Chile was described, it was considered to be a closely related species (Malme 1925). The poorly known species *P. fuegiense* (Zahlbr.) Henssen & P. M. Jørg. also needs to be evaluated in this context. It has not been studied in modern times, except for being transferred from *Pannaria* to *Psoroma* by Jørgensen (1999), and positioned in phylogenetic trees by Ekman & Jørgensen (2002) and Passo *et al*. (2008).

During our own field studies in the Juan Fernández Islands, *Psoroma pholidotum* proved to be a greenish species, and both dry and up to two year old herbarium specimens look superficially quite similar to *Psoroma soccatum*, except for the soredia in the latter. Therefore, this study also includes this last

species and also the other usnic acid-containing species, until now treated mainly as *P. pholidotoides*. They have been considered to be rather well-known species with a distinct chemistry. The aim of the present study is therefore to describe the accepted species of these two groups in relation to other species of *Psoroma*, and to define their genetic positions supported by a phylogenetic analysis based on ITS and LSU rDNA.

Materials and Methods

Specimens and DNA extraction

Thirty-nine specimens representing five *Pannaria* species and ten *Psoroma* species were analyzed in this study (Table 1). Voucher specimens of all samples are deposited at TROM, and Antarctic specimens also at Korea Polar Research Institute. Collection information is included in Table 1. Collection information on the additional GenBank samples added in Fig. 2 has recently been presented by Passo *et al.* (2008) and is not included here. *Protopannaria pezizoides* was included to root the tree.

The lichen materials were ground using a freeze-crusher (SK200, Tokken, Japan) after freezing in liquid nitrogen, and genomic DNAs were extracted using Plant DNA mini-kit (Qiagen, Germany) according to the manufacturer's guide.

PCR amplification and sequencing

ITS1-5.8S-ITS2 and partial LSU rDNA (1-948 nucleotide positions, *S. cerevisiae* numbering) were amplified using the primers ITS1F (5′-CTT GGT CAT TTA GAG GAA GTA A-3′) (Gardes & Bruns 1993) and LR5 (5′-ATC CTG AGG GAA ACT TC-3′) (Vilgalys & Hester 1990). Touch-down PCR amplifications were performed in a T-gradient thermocycler (Biometra, Germany) with the following cycling parameters: 5 min. initial denaturation at 94°C, 15 touch-down cycles of 30 s. denaturation at 94°C, 1 min annealing at 62–55°C at the ramp of 0.5° per cycle and 2 min extension at 72°, followed by 30 cycles of 30 s. denaturation at 94°C, 1 min annealing at 55°, and 1 min extension at 72°, and 10 min. final extension at 72°. Sequences of ITS and LSU rDNA regions were determined with primers, ITS1F, ITS4 (TCC TCC GCT TAT TGA TAT GC) (White *et al.*, 1990), LR0R (5′-GTA CCC GCT GAA CTT AAG C-3′) (Rehner & Samuels 1994), and LR5 using ABI 3730XL automated sequencer (Applied Biosystems, USA). The sequences were proof read, edited and aligned using the jPHYDIT program (Jeon *et al.*, 2005).

Phylogenetic analysis

Sequence alignment of ITS1, 5.8S, ITS2 and partial LSU rDNA were conducted by the program ClustalX ver. 1.83 (Thompson *et al.* 1997) and manually adjusted. Ambiguously aligned sites were excluded from the phylogenetic analyses. Phylogenetic trees were inferred from the data sets by neighbor-joining (NJ), maximum parsimony (MP), and maximum likelihood (ML) analyses. NJ tree was reconstructed using NJ algorithm of PAUP 4.0b10 (Swofford 2002) under the Kimura's 2-parameter model (Kimura 1980). Maximum parsimony analysis was conducted by heuristic search option of PAUP 4.0b10 with 1000 replicates of random sequence additions, tree bisection reconnection (TBR) branch swapping algorithm, and MulTrees options in effect. All gaps were treated as missing data. Weighted MP analysis (wtMP) was conducted after weighting characters by rescaled consistency index (RC) values with the same search parameters as MP analysis. ML tree was searched by PhyML ver 3.0 (Guindon & Gascuel, 2003) with the HKY evolutionary model (Hasegawa *et al.* 1985) and the search options of best tree topology finding by branch swapping of NNIs and SPRs, initial tree constructed by BioNJ method, and parameter estimation for proportion of invariant and transition/transversion ratio. Supports for internal branches were tested by the bootstrap analyses of 1000 and 100 replications for MP and ML searches, respectively.

Morphological and anatomical analysis

Type material of most of the species studied, in addition to our own collections and selected collections from other herbaria, were subjected to morphological, anatomical and chemical studies and compared with related species from our own and other collections available. Chemistry was studied using standard TLC methods based on Culberson (1972) and Orange *et al.* (2001), involving solvents A and C. Iodine+ reactions were studied by adding IKI to mounts pretreated with KOH (Orange *et al.* 2001), but perispore structures were studied on material mounted in water only. Nomenclature of ascospore structures follows Nordin (1997). Because of the challenges in separating the species, anatomical comparisons were particularly thorough with copies of detailed drawings of 6–15 spores and IKI+ ascus structures of all cited specimens with mature apothecia enclosed with the herbarium specimens.

Results

PCR and sequencing

Approximately 1·5 kb DNA fragments were amplified from most of the specimens with the primers ITS1F and LR5, but size variation was observed in some of the specimens with larger DNA fragments ranging

TABLE 1. *Details of* Pannaria *and* Psoroma *specimens and GenBank accession numbers of the ITS and LSU rDNA sequences generated for this study*

Species name and voucher number	Geographical origins	Introns♣ (size, bp)	GenBank Acc. number
Pannaria andina P.M. Jørg. & Sipman			
NK-43 (*A. Elvebakk* 06:245)	CHILE: Juan Fernández Archipelago, Isla Robinson Crusoe		CQ927268
Pannaria pallida (Nyl.) Hue			
NK-83 (*A. Elvebakk* 07:229F)	CHILE: XI Región Aysén, Puente los Ñadis, 55 km S of Cochrane	SSUi (273)	CQ927270
Pannaria rubiginella P.M. Jørg. & Sipman			
NK-45 (*A. Elvebakk* 06:241A)	CHILE: Juan Fernández Archipelago, Isla Robinson Crusoe		CQ927269
Pannaria rubiginosa (Ach.) Bory			
NK-01 (*A. Elvebakk* 04:009)	NORWAY: Nordland, Hamarøy, Kvannvatnet		CQ927267
Pannaria sphinctrina (Mont.) Tuck.			
NK-18 (*A. Elvebakk* 06:384)	CHILE: Juan Fernández Archipelago, Isla Robinson Crusoe	SSUi (278), LSUi1 (65)	CQ927271
Protopannaria pezizoides (G.H. Web.) P.M. Jørg & S. Ekman			
NK-65 (*A. Elvebakk* 03:303)	NORWAY: Nordland, Bodø, Ausvika		CQ927266
Psoroma buchananii (C. Knight) Nyl.			
NK-29 (*A. Elvebakk* 00:819)	CHILE: XII Region de Magallanes, Parque Nacional Pali-Aike		CQ927298
NK-33 (*A. Elvebakk* 00:830)	CHILE: XII Región de Magallanes, Parque Nacional Pali-Aike		CQ927299
NK-34 (*A. Elvebakk* 00:858)	CHILE: XII Región de Magallanes, Parque Nacional Torres del Paine		CQ927300
Psoroma cinnamomeum Malme			
NK-30 (*A. Elvebakk* 00:829)	CHILE: XII Región de Magallanes, Parque Nacional Pali-Aike	SSUi (335)	CQ927293
NK-37 (*A. Elvebakk* 99:676)	CHILE: XII Región de Magallanes, Estrecho de Magallanes, Punta Valle	SSUi (>332), LSUi2 (55)	CQ927292
Psoroma contextum Stirt.			
NK-77 (*A. Elvebakk* 07:323B)	CHILE: IX Región de la Araucanía, Parque Nacional Nahuelbuta	LSUi1 (>59)	CQ927274
Psoroma cf. *contextum*			
NK-79 (*A. Elvebakk* 98:046)	CHILE: XII Región, Provincia Ultima Esperanza, Parque Nacional Torres del Paine		CQ927273
NK-102 (*A. Elvebakk* 08:061)	AUSTRALIA: Victoria, Tarra Bulga National Park	LSUi1 (>22)	CQ927276
NK-49 (*A. Elvebakk* 06:338)	CHILE: Juan Fernández Archipelago, Isla Robinson Crusoe		CQ927272
NK-78 (*A. Elvebakk* 07:370)	CHILE: IX Región de la Araucanía, Reserva Nacional Malalchuello	SSUi (263)	CQ927275
NK-105 (*A. Elvebakk* 08:148)	AUSTRALIA: Victoria, Errinundra National Park	LSUi1 (>22)	CQ927277
Psoroma fruticulosum P. James & Henssen			
NK-32 (*A. Elvebakk* 99:1093)	CHILE: XII Región de Magallanes, Parque Nacional Torres del Paine		CQ927301
NK-35 (*A. Elvebakk* 98:241)	CHILE: XII Región de Magallanes, Parque Nacional Torres del Paine		CQ927302
NK-36 (*A. Elvebakk* 98:421)	CHILE: XII Región de Magallanes, Parque Nacional Torres del Paine		CQ927303

TABLE 1. *Continued*

Species name and voucher number	Geographical origins	Introns♣ (size, bp)	GenBank Acc. number
Psoroma fuegiense (Zahlbr.) Henssen & P.M. Jørg.			
NK-75 (*A. Elvebakk* 07:107B)	CHILE: XI Región Aysén, Valle Explotadores		CQ927284
NK-76 (*A. Elvebakk* 07:220)	CHILE: XI Región Aysén, Puente los Ñadis, 55 km S of Cochrane		CQ927285
Psoroma hypnorum (Vahl) S.F. Gray			
NK-03 (*S. R. Karlsen* s.n.)	NORWAY: Finnmark, Berlevåg, Trollfjorden	SSUi (256)	CQ927294
HSG080110-30	ANTARCTICA: King George Island, Barton Peninsula		CQ927295
HSG080111-12	ANTARCTICA: King George Island, Barton Peninsula		CQ927296
PCH080113-23	ANTARCTICA: King George Island, Barton Peninsula		CQ927297
Psoroma paleaceum (Fr.) Nyl.			
NK-31 (*A. Elvebakk* 95:350)	CHILE: XII Región de Magallanes, Parque Nacional Torres del Paine		CQ927304
HSG080124-16	CHILE: XII Región de Magallanes, near Punta Arenas	SSUi (300)	CQ927305
Psoroma pholidotum (Mont.) Müll. Arg.			
NK-46 (*A. Elvebakk* 06:336)	CHILE: Juan Fernández Archipelago, Isla Robinson Crusoe	LSUi 1(54)	CQ927286
NK-47 (*A. Elvebakk* 06:330)	CHILE: Juan Fernández Archipelago, Isla Robinson Crusoe	LSUi 1(54)	CQ927287
NK-52 (*A. Elvebakk* 06:385)	CHILE: Juan Fernández Archipelago, Isla Robinson Crusoe	LSUi 1(54)	CQ927288
NK-53 (*A. Elvebakk* 06:390A)	CHILE: Juan Fernández Archipelago, Isla Robinson Crusoe	LSUi 1(54)	CQ927289
Psoroma soccatum R. Br. ex Cromb.			
NK-25 (*A. Elvebakk* 06:230)	CHILE: Juan Fernández Archipelago, Isla Robinson Crusoe		CQ927278
NK-26 (*A. Elvebakk* 06:406)	CHILE: XI Región Aysén, Valle de Río Simpson		CQ927279
NK-27 (*A. Elvebakk* 06:471A)	CHILE: XI Región Aysén, near the village Río Cisnes		CQ927280
NK-28 (*A. Elvebakk* 06:401)	CHILE: XI Región Aysén, Valle de Río Simpson		CQ927281
NK-104 (*A. Elvebakk* 08:035)	AUSTRALIA: Victoria, Baw Baw National Park		CQ927282
NK-106 (*A .Elvebakk* 08:146)	AUSTRALIA: Victoria, Errinundra National Park		CQ927283
Psoroma tenue Henssen			
HSG080113-14	ANTARCTICA: King George Island, Weaver Peninsula	SSUi(335), LSUi2 (56)	CQ927290
HSG080113-17	ANTARCTICA: King George Island, Weaver Peninsula	SSUi(335), LSUi2 (56)	CQ927291

between 1·6 kb and 1·85 kb (data not shown). Sequence alignment with reference sequences revealed that size variation was mostly caused by the presence/absence of intron sequences after 1770 nt position (SSUi; *S. cerevisiae* numbering) of SSU rDNA and/or after 915 and 917 nt positions (LSUi1 and LSUi2; *S. cerevisiae* numbering) of LSU rDNA (Table 1).

Phylogenetic analysis

Combined sequences of ITS1-5.8S-ITS2-partial LSU rDNA sequences excluding intron sequences and ambiguously aligned nucleotide sites constituted a total of 1344 characters. Among them 1102 sites were constant, 56 sites were variable but parsimony-uninformative, and 186 sites were parsimony-informative characters. The ML tree is presented with bootstrap support values by ML, MP, wtMP, and NJ searches in Fig. 1. Strict consensus of six and two equally parsimonious trees by MP and weighted MP analyses and NJ tree were very similar to the tree by ML search. Branches conserved in four independent phylogenetic analyses were presented as thick lines. Most of the branches that were strongly supported by high bootstrap values were maintained in trees by different phylogeny methods. Disagreement among trees was found in relationships among samples of *Psoroma contextum* and among samples of *P. hypnorum* from the Antarctic. The difference was also found in the position of *Pannaria sphinctrina* NK18 and *Pannaria pallida* NK83. Phylogenetic trees reconstructed using the ITS region and LSU rDNA separately, maintained the relationships of main lineages which were conserved in combined sequence analyses (data not shown).

In the phylogenetic trees by ML, MP, wtMP and NJ analyses, *Pannaria* species and *Psoroma* s. lat. species were clearly distinguished. Monophyly of each lineage was strongly supported by high bootstrap values. Within the *Psoroma* s. lat. lineage, corticolous species were separated from the terricolous species. The *Xanthopsoroma* lineage was composed of the corticolous species, *Psoroma soccatum* and *P. contextum*, and monophyly of the lineage was supported by 100% bootstrap values. The two species *P. soccatum* and *P. contextum* s. lat. were also clearly separated. The *Psorophorus* lineage was composed of *Psoroma pholidotum* and *P. fuegiense*, also corticolous species, and monophyly of the lineage was supported by 100% bootstrap value. The species were also very well separated. The *Psoroma* s. str. lineage was composed of terricolous species from Chile, Norway and the Antarctic. Monophyly of the lineage was maintained in ML, MP, wtMP and NJ trees and bootstrap support was moderate (ML, MP and NJ) or high (wtMP). *Psoroma cinnamomeum* and *P. tenue* formed two clades well isolated from other species within *Psoroma* s. str. The samples of *P. buchananii*, *P. fruticulosum* and *P. paleaceum* formed strongly supported monophyletic species clades, whereas the only European sample of *P. hypnorum* included, did not associate well with the Antarctic samples. *Psoroma buchananii* is reported as new to Chile here.

ITS sequences from this study and others retrieved from GenBank database were aligned together and phylogeny was reconstructed by the NJ method (Fig. 2). In this analysis, the four main lineages defined by combined sequences of ITS and LSU rDNA (Fig. 1) were maintained. Supports for the monophyly of *Xanthopsoroma* and *Psorophorous* clades were relatively high (77% and 100%), but supports for the monophyly of *Pannaria* s. lat. and *Psoroma* s. str. were low (<50% and 58% respectively). Within the *Pannaria* clade, the five samples included in Fig. 1 grouped nicely with samples from the same or closely related species in the corresponding clade of Fig. 2, now numbering 20 samples. The two GenBank sequences added to the *Xanthopsoroma* clade were almost identical to sequences included in Fig. 1. The same was the case in the *Psorophorus* clade, although a sample previously analyzed phylogenetically as *Psoroma pholidotum* (Passo *et al.* 2008), grouped with *fuegiense* instead of *pholidotum*. The GenBank sequence of *P. paleaceum* grouped nicely with the two sequences already included in Fig. 1,

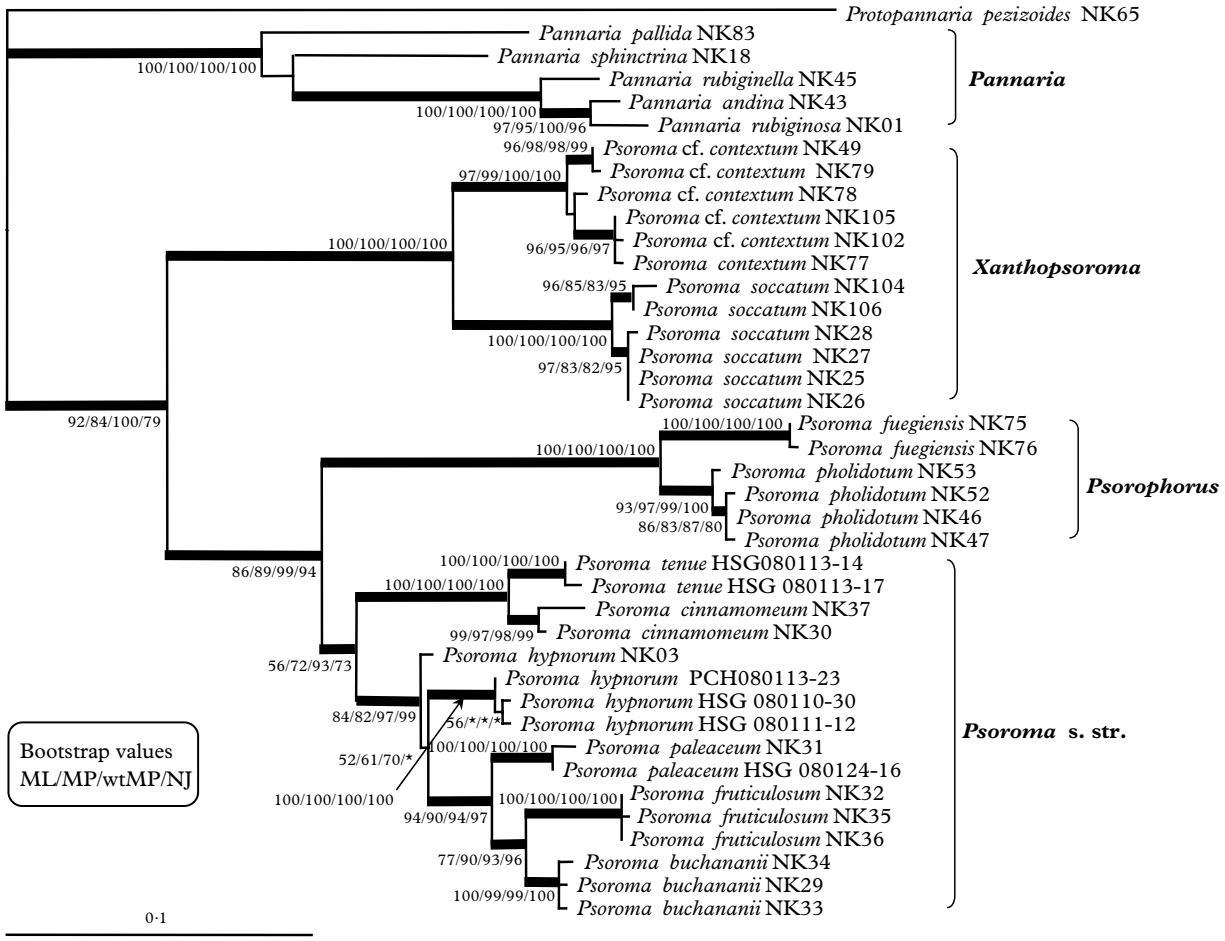

FIG. 1. Maximum likelihood tree based on combined sequences of ITS1-5.8S-ITS2-partial LSU rRNA gene. Branches that were conserved in ML, MP,wtMP and NJ are represented as thick lines. Bootstrap values are indicated when values were above 50%.

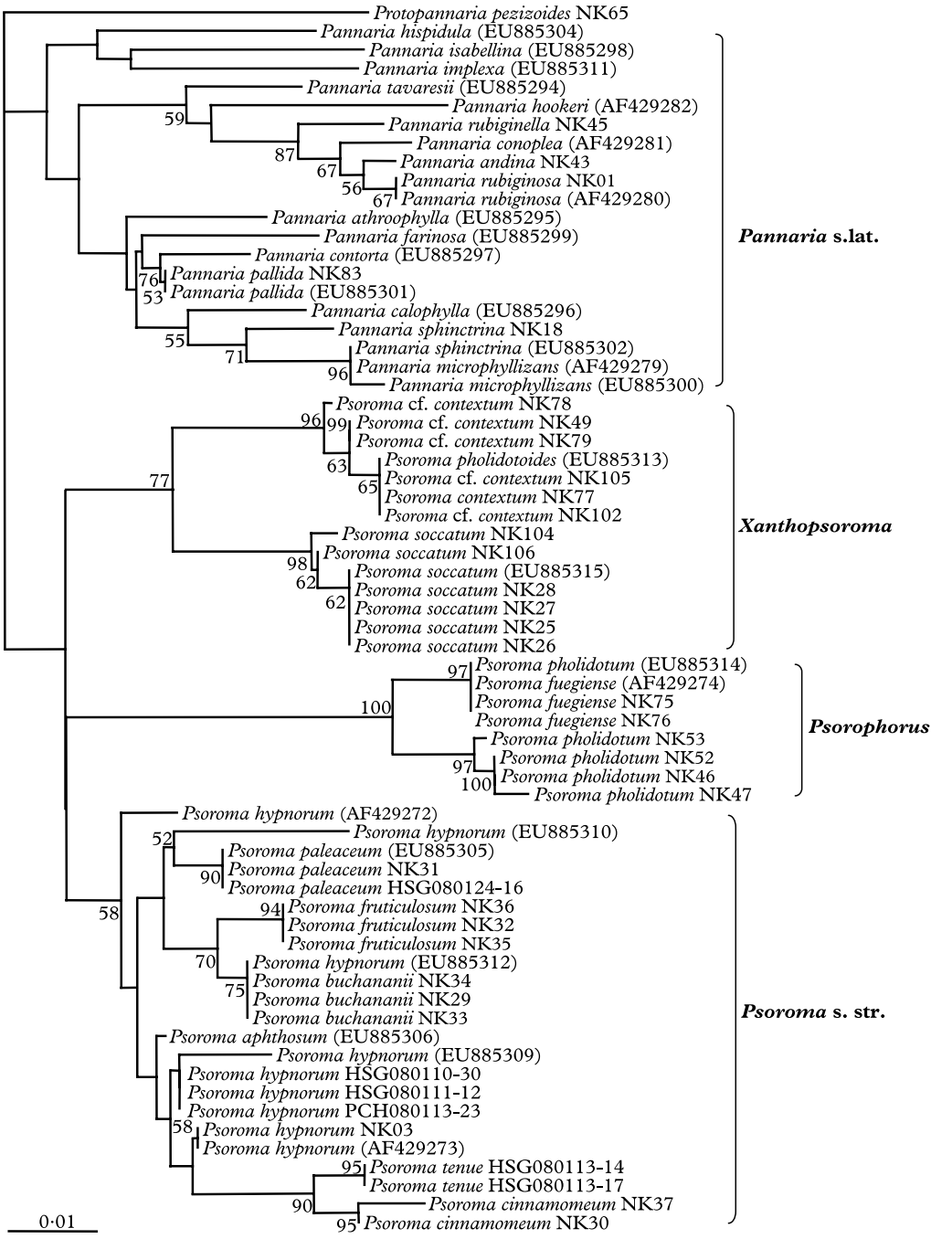

FIG. 2. Neighbor-joining tree based on the ITS1-5.8S-ITS2 rRNA sequences. Accession numbers are included for the sequences retrieved from GenBank. Bootstrap values are indicated when values were above 50%.

whereas *P. hypnorum* is more heterogeneous after the addition of another three GenBank sequences, in addition to one more sequence (EU885312) appearing in Fig. 2 as a possibly misidentified specimen of *P. buchananii*.

The Genera and the Species

Psorophorus Elvebakk & Hong gen. nov.

Psoromati sensu stricto (ut *Psoroma hypnorum* id definit) similis, sed corticola plerumque, hypothallo vel prothallo nigro distincto, squamulis et cephalodiis tenuibus et valde ad substratum adpressis, structura ascorum amyloidea interna tubuliformi instructus, et melaninis destitutus.

Generitypus: Psorophorus pholidotus (Mont.) Elvebakk (2010).

Thallus squamulose, 2–15 cm wide, corticolous. *Chlorobiont squamules* 70–100 μm thick, densely appressed to the substratum, up to 1 mm wide but mostly 0·1–0·5 mm, circular to irregularly incised, discrete, becoming confluent centrally, strongly salad green when wet, distinctly pale greenish when dry, a colour maintained in specimens several years old but which turn olive-brown after decades of storage. *Hypothallus* 10–15 μm thick, very distinct and black, protruding into a 2–5 mm wide prothallus, also present below squamules. *Upper surface* glabrous and glossy. *Epicortex* 15–20 μm thick, of thin-walled (*c.*1 μm thick) cells, 3–5 μm in size. *Chlorobiont* of *cf. Myrmecia* cells, irregularly globose to ellipsoid, 6–12 × 7–13 μm in size, chlorobiont layer 50–70 μm thick. *Medulla* 10–15 μm thick. *Hypocortex* lacking. *Cephalodia* grey, very abundant, located directly on the prothallus/hypothallus, very rarely on squamules, 0·6–1·2 mm wide, when young more or less placodioid, later developing small erect lobules. *Cyanobiont Nostoc,* cells greyish green, irregularly subglobose or ellipsoid, 3–6 × 4–7 μm in size, in 20–40 μm large, indistinct glomeruli, without visible chain structures.

Apothecia sessile to subsessile, laminal, 0·8–1·5 mm wide. *Discs* at first dark chestnut brown or almost blackish, gradually becoming pale brown with an orange to reddish tinge, and flat or convex when old. *Thalline excipulum* 40–120 μm wide on mature apothecia when seen from above, crenulate-striate, with anatomy as in the squamules, irregular and present or evanescent on older apothecia, basal parts mostly hirsute. *Epithecium* light brown, *c.* 10 μm thick. *Hymenium* colourless, but strongly IKI + blue, *c.* 80 μm thick. *Asci* clavate, 15 × 70–80 μm in size, with 8 ascospores and a tube-like, IKI+ blue, apical structure, sometimes with one or two additional cap-like structures. *Proper ascospores* hyaline, non-septate, subglobose to ellipsoid, 12–20 × 6·5–12 μm. *Perispores* of the same shape, 12–22 × 7–13 μm, distinctly verrucose, commonly with thick, nodulose apical extensions, 2·5–4 μm in size. *Paraphyses* 4–5-septate, simple to sparingly branched, apices 2–4·5 μm wide, distinctly swollen with short articulated segments. *Hypothecium* light brown, *c.* 70 μm thick, IKI negative.

Chemistry. No compounds detected by TLC, and no visible melanins/pigments except in the apothecia.

Etymology. The name refers to the very distinct and black hypothallus/prothallus 'carrying' discrete squamules and cephalodia.

Key to the species of *Psorophorus*

1 Cephalodia pale grey, rosettiform to umbilicate when young; mature apothecia strongly convex with evanescent margins, long-ellipsoid, often rather irregular proper ascospores, and perispores commonly with nodulose apical extensions . . . . . **P. pholidotus**

Cephalodia dark grey, irregularly cushion-formed when young; mature apothecia weakly convex without evanescent margins, subglobose to short-ellipsoid proper ascospores, and perispores without nodulose apical extensions . . **P. fuegiense**

Psorophorus pholidotus (Mont.) Elvebakk comb. nov.

Basionym: *Parmelia pholidota* Mont., *Annls. Sci. Nat. Bot. Ser. 2*, **4:**18 (1835); type: Ins. Juan Fernández, in cortice *Drymis* (canelo), April 1830, *Bertero* 1626 (PC-MONT, 'holotype' (Jørgensen 2003), here selected as neotype). —*Pannaria pholidota* (Mont.) Nyl., *Annls. Sci. Nat. Bot. Sér.4*, **3***:* 182 (1855).—*Psoroma pholidotum* (Mont.) Müll. Arg., *Flora* **71:** 45 (1888).

Pannaria reticulata Hue, *Nouv. Arch. Mus. Nat. Hist. Paris Sér. 4*, **8:** 261 (1906), nom. superf., see Jørgensen (2003: 71).—*Psoroma reticulatum* (Hue) Zahlbr., *Catal. Univ. Lich*. **III:** 294 (1925), nom. superf., see Jørgensen (2003: 71).

Notes on typification. Jørgensen (2003) cited the type as "Juan Fernández, ad corticem Drymidis, April 1830, *Bertero* 1626 (PC-MONT, holotype !)". However, Montagne (1835) did not mention *Bertero* 1626, but only cited *Bertero* 1623, "crescit ad corticem *Drymis chilensis*, vulgò *Canelo*". Searches in PC only revealed an unnumbered Bertero collection 'ex *Psidium*', and *Bertero* 1626. The latter carries the information "In cortice *Drymis* (canelo), Ins. Juan Fernandez, 1830 april". According to D. J. Galloway (pers. comm.) this has been written in Bertero's handwriting, but there is no evidence of Montagne's handwriting. There is a possibility that Montagne (1835) erroneously wrote '1623' instead of '1626'. Gay (1852: 147) in his survey of Chilean lichens cited both *Bertero* 1623 and 1626 as collections of this species. The same is the case with Zahlbruckner (1924). However, the *Bertero* 1623 collection was not cited by Hue (1908) who studied *P. pholidotus* extensively. It probably does not exist, not in H-NYL either. In conclusion, *Bertero* 1626 is defined as a neotype here. Both PC collections are in good agreement with the collections of the species made recently in the Juan Fernández Islands.

(Figs 3A, 4A & 5A)

Characters as stated for the genus, except for the following:

Cephalodia pale grey, when young regularly rosettiform, placodioid to weakly umbilicate, later developing small erect lobules. *Apothecium discs* developing a strong convexity when old. *Thalline excipulum* mostly evanescent on older apothecia. *Asci* with a short and broad, tube-like, IKI+ blue, apical structure. *Proper ascospores* long-ellipsoid, often weakly lacrymiform or weakly acuminate, 14–20 × 6·5–10 µm; *perispores* of the same shape, 16–22 × 7–12 µm, distinctly verrucose, commonly with thick, nodulose 2·5–4 µm apical extensions.

Additional specimens studied. **Chile:** *Arquipiélago de Juan Fernández*: Isla Robinson Crusoe, Miradór de Selkirk and 0·5 km E of Miradór de Selkirk, 33°38′S, 78°51′W, 2006, *A. Elvebakk* 06:311 (SGO); 06:315; 06:319A; 06:330; 06:336; 06:337 (TROM); 1·5 km W of San Juan Bautista, 33° 38′S, 78° 50′W, 2006, *A. Elvebakk* 06:257 (TROM); Plazoleta del Yunque, 33°38′S, 78° 50′W, 2006, *A. Elvebakk* 06:385; 06:386; 06:390A; 06:393; 06:394 (TROM); 06:397 (UPS); Cordón Pesea de los Viejos, 1975, *W. Quilhot* s.n. (UV). *XIV Región de los Ríos*: Lago Riñihue, Riñihue, Cerro Tralcan, 1940, *R. Santesson* 3805 (S). *X Región de los Lagos*: Chiloé, Cucao, Parque Nacional de Chiloé, near Guardería, at Tepual path, 42° 37′S, 74° 06′W, 2000, *A. Elvebakk* 00:521 (TROM). *XI Región Aysén*: 14 km E of Tortel, 47° 47′S, 73° 23′ W, 2007, *A. Elvebakk* 07:246 (TROM).

Psorophorus fuegiensis (Zahlbr.) Elvebakk & Hong comb. nov.

Basionym: *Pannaria fuegiensis* Zahlbr., *Kungl. Sv. Vetensk.-Akad. Handl*. **57**(6)**:** 13 (1917); type: (Chile): Feuerland, im Walde inweit der Mündung des Rio Azopardo, auf Baumrinden (W— holotype!).—*Psoroma fuegiense* (Zahlbr.) Henssen & P. M. Jørg. (as "*fuegense*"), *New Zeal. Journ. Bot*. **37:** 261 (1999).

Psoroma microlepideum Malme, *Ark. Bot*. **20; 6:** 17 (1925);—type: 'Patagonia occident., Isla Desolacion, Puerto Angosto (Chile), Dusén Fueg. # 215 (S—holotype!), syn. nov.

Psoroma microlepideum var. *pallidum* Räsänen, *Ann. Bot. Soc. Zool.-Bot. Fenn. 'Vanamo'* **2, I-VI:** 45 (1932); —type: Chile, Fuegia occ., Fiordo Finlandia, Bahia Kairamoi, in silva paludosa *Nothofagi antarcticae* ad corticem arboretum, 3 March 1929, *H. Roivainen* (H—holotype).

(Figs. 3B, 4B & 5B)

Identical or broadly overlapping with characters of *P. pholidotus*, except in the following:

Cephalodia dark grey, starting as irregular, placodioid, weakly convex cushions, gradually developing small erect lobules and becoming similar to those of *P. pholidotus*. *Apothecia* remaining rather flat or only weakly convex when mature. *Thalline excipulum* rarely evanescent on old apothecia. *Asci* with a small and narrow, tube-like IKI + blue apical structure. *Proper ascospores* subglobose to short-ellipsoid 10–17 × 9–12 µm, never lacrymiform nor apiculate; *perispores* 12–19 × 10–13 µm, rarely with any apical extensions.

FIG. 3. *Psorophorus* species. A, *P. pholidotus* photographed of an almost 3-year old herbarium specimen (*A. Elvebakk* 06:336); B, *P. fuegiensis* (holotype).

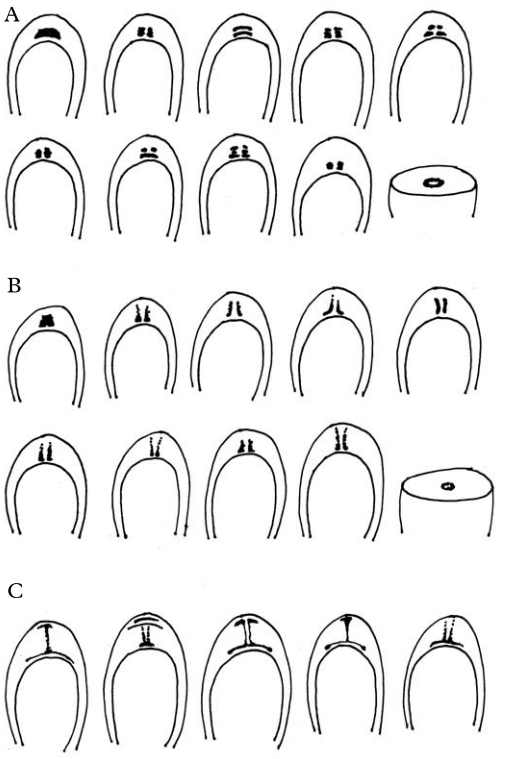

FIG. 4. IKI+ ascus apical tube structures. A, *Psorophorus pholidotus* (the first one studied with high IKI concentration); B, *P. fuegiensis* (the first one studied with high IKI concentration); C, *Psoroma hypnorum*. Scale = 10 μm.

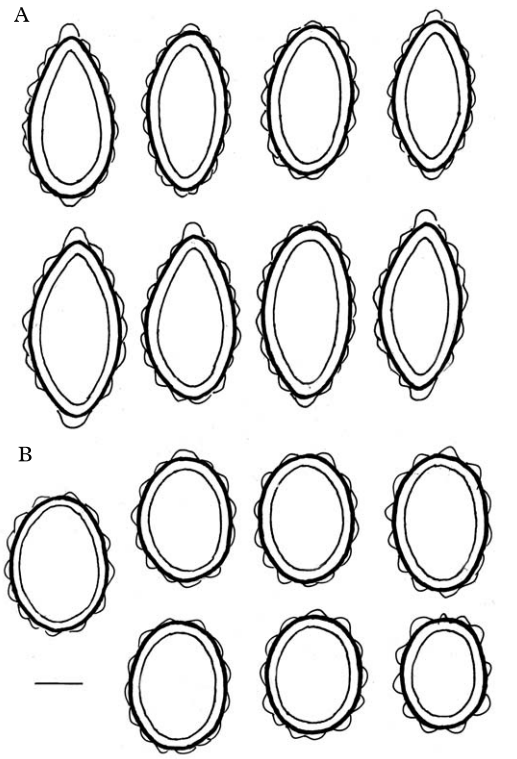

FIG. 5. *Psorophorus*, ascospores. A, *P. pholidotus*; B, *P. fuegiensis*. Scale = 5 μm.

Additional specimens studied. **Chile:** *IX Región de la Araucanía*: Parque Nacional Conguillío, 1986, *W. Quilhot* s.n. (UV); Road from Melipeuco to Lago Conguillío, road to Administration Centre, 38° 49′ S, 71° 40′ W, 1986, *B. J. Coppins, D. J. Galloway, G. Guzmán* & *P. W. James* 5647 (BM). *X Región de los Lagos*: Provincia de Llanquihue, Parque Nacional Vicente Pérez Rosales, near Petrohué, 41°09′ S, 72°23′W, 2001, *J. W. Bjerke* 517/01 (TROM); 2000, *A. Elvebakk* 00:570 (TROM). *XIV Región de los Ríos*: Lago Riñihue, Enco, 1940, *R. Santesson* 7616a (S); Lago Panguipulli, Volcán Choshuenco, 1940, *R. Santesson* 3938B (S); 11·4 km SW of Choshuenco near Río Enco, 39° 53′ S, 72° 81′ W, 1986, *B. J. Coppins, D. J. Galloway, G. Guzmán* & *P. W. James* 4143 (BM). *XI Región Aysén*: Laguna San Rafael National Park, on slope N of Río Salton, 46° 38′ N – 73° 51′W, 1997, *M. Wedin* 6104, 6108 (BM); 38 km along the road N of Bahía Murta, 5 km W of Laguna Cofré, 46°11′S, 72°45′W, 2007, *A. Elvebakk* 07:312B (TROM); Valle Explotadores, Cabañas Alacaluf, 45 km along the road west of Puerto Tranquilo, 46°30′ S, 73°04′W, 2007, *A. Elvebakk* 07:098; 07:107B (TROM); 55 km SW along the road of Cochrane, 3·5 km N of Puente Los Ñadis, 47°35′ S, 72°52′W, 2007, *A. Elvebakk* 07:220 (SGO, TROM, UPS); 7 km N of the road junction Tortel and Puerto Yungai, 47°44′ S, 73°14′W, 2007, *A. Elvebakk* 07:267B (TROM); 0·5 km E of Tortel, 47° 47′ S, 73°31′W, 2007, *A. Elvebakk* 07:233B (TROM); 4 km E of Tortel, 47° 48 S, 73° 29′ W, 2007, *A. Elvebakk* 07:236A (TROM).

Discussion of *Psorophorus* species

All the names in this group have been widely misunderstood, particularly in terms of their photobiont associations. Zahlbruckner (1917) interpreted his *Pannaria fuegiensis* as a bipartite cyanospecies, whereas Malme (1925) described the now synonymous *Psoroma microlepideum* as a green algal species without any cephalodia observed. Nylander (1855*a*, 1859, 1863) evidently considered *Psorophorus pholidotus* to be a bipartite cyanospecies, as he separated the genera *Psoroma* and *Pannaria* principally on their choice of

photobionts, and treated this species as *Pannaria pholidota*, a combination overlooked in recent treatments. This probably explains why he also reported the species from Mexico (Nylander 1859), an area with many bipartite species, but lacking tripartites. Hue (1892, 1902, 1908) continued this interpretation, but with *Pannaria* now in a broader sense, and cited it from the island Sao Tomé off West Africa, Bolivia and Sri Lanka ('Ceylon'), and provided a very thorough description, including cephalodia. One Sri Lankan collection (*Thwaites* 52, S) has been seen by us, and corresponds to the Palaeotropical '*Psoroma sphinctrinum*' complex, which is planned to be accommodated in a new genus by A. Elvebakk & P. M. Jørgensen (unpublished).

The species has also been confused with *Xanthopsoroma*. Nylander (1855*b*, 1863) reported a collection from the mainland Chilean cordillera as *P. pholidota* (*Lechler* 853, not studied by us). Hue (1902) indicated that this collection, together with a Gay collection from southern Chile, represented a new species, named *Pannaria reticulata* Hue, however, invalidly, because no description was given at the time. When the description was provided later (Hue 1906), he included the name *Pannaria pholidota* (Mont.) Nyl. as a synonym, and his new species, apparently meant for what we treat here as *Xanthopsoroma contextum,* therefore became a synonym and a nom. superf. for *P. pholidotus*, a conclusion already stated by Jørgensen (2003).

Our studies have shown *Pannaria fuegiensis* and *Psoroma microlepideus* to be conspecific, with the former name taking priority. Also original spore measurements published by Zahlbruckner (1917) and Malme (1925) are very similar. The holotype of *Pannaria fuegiensis* has a somewhat broader and more robust thalline excipulum than the holotype of *Psoroma microlepideum* and most other specimens initially determined accordingly, with the exception of *Quilhot* s.n. However, their anatomy and other characters are identical and the thalline excipulum character is not considered sufficient to merit their recognition as separate species.

The type of *Parmelia pholidota* is very similar in habit to the types referred to above. Except for their type collections, these species have previously been interpreted so variably that no records are reliable. Malme (1925) wrote, even on the label of the holotype specimen of *Psoroma microlepideum*, that it might be conspecific with *Psoroma pholidotum*. A second specimen of *Psoroma fuegiense* was recorded from Ushuaia by Malme (1925). It was, however, redetermined as *Fuscopannaria minor* (Darb.) P. M. Jørg. by Jørgensen (1999). The report from the Juan Fernandez Islands by Zahlbruckner (1924) is probably also erroneous. Räsänen (1932) described *P. microlepideum* var. *pallida,* characterized by a whitish pale thallus, but it has already been included in *P. microlepideum* by Jørgensen (2003). Follmann (1965) accepted *P. microlepideum* as a separate rare species, known only from the Region of Magallanes, whereas *Psoroma pholidotum* was also considered to be uncommon, but with a wide distribution in mainland Chile in addition to its occurrence in the Juan Fernández Islands. *Psoroma pholidotum* has been accepted for Argentina by Grassi (1950), Calvelo & Liberatore (2002) and Passo *et al.* (2008), but these records need to be confirmed.

In the present study *Psorophorus pholidotus* and *Psorophorus fuegiensis* are genetically very distinct. Morphologically, the characters cited are quite good, but not completely reliable. An *a posteriori* determination test on the 37 collections studied showed that about 85 % of them could be determined on the external apothecium and/or cephalodium characters alone, including several collections from the Juan Fernández Islands where mature apothecia were lacking or poorly developed. It is now shown here that they are very distinct anatomically. Short-ellipsoid vs. long-ellipsoid spores is a very reliable character. The size ranges quoted represent 98% of the measurements. Whereas *P. fuegiensis* spores are always very regularly elliptic, those of *P. pholidotus* are frequently either weakly apiculate or lacrymiform.

Surprisingly, we also found clear differences between the two species in the IKI+

ascus apical structures. Cross- and longitudinal sections show a distinct tube structure in both species, which is broad in *P. pholidotus*, sometimes with additional sheet structures, and narrower in *P. fuegiensis*. This is a character which has only been previously used at generic or sectional level in *Pannariaceae*, but is now found to be taxonomically very important at the species level. The IKI+ difference may be considered as the strongest visible manifestation that these two species are very distinct in spite of their morphological similarity. Interestingly, both recent collections used in the phylograms by Ekman & Jørgensen (2002) and Passo *et al.* (2008) can, quite unambiguously, be confirmed by our phylogenetic reanalysis to represent *Psorophorus fuegiensis* (*Passo* 126, published as *Psoroma pholidotum*, and *Wedin* 6108, published as *P. fuegiense*).

Psorophorus pholidotus is very common on Isla Robinson Crusoe, but it is not a Juan Fernández endemic. Three well-defined specimens have been studied from the Chilean mainland (from Regions XIV, X and XI), but *P. fuegiensis* is a far more common species there; it is listed from Regions IX–XII and the recently established Region XIV (between IX and X). It is probably widespread also in the austral, wettest forests of Argentina, but no specimens have been seen by us. The genus *Psorophorus* is a southern South American endemic.

Xanthopsoroma Elvebakk & Hong gen. nov.

Psoromati sensu stricto (ut *Psoroma hypnorum* id definit) simile, sed corticola plerumque, hypothallo vel prothallo nigro distincto, squamulis valde ad substratum adpressis, perisporis planis et magnis extensionibus apicalibus nodulosis sive truncatis praeditis, structura ascorum interna tubiformi amyloidea valde distincta et tholo generatim IKI+ circumdata instructum, acidum usneicum et nonnulla terpenoida incognita continens.

Generitype: *Xanthopsoroma contextum* (Stirt.) Elvebakk (2010).

Thallus squamulose, 2–15 cm wide, corticolous, occasionally saxicolous. *Chlorobiont squamules* 120–180 µm thick, appressed to the substratum, in peripheral parts up to 2 mm wide, in central parts strongly imbricate, yellowish green, turning more yellow to ochraceous after decades of storage. *Hypothallus* very distinct and black, protruding into a 2–5 mm wide prothallus. *Upper surface* glabrous and glossy. *Epicortex* 40–60 µm thick, paraplectenchymatous, cell walls 3–4 µm thick, lumens 5–10 µm, the lowermost elongated and directed towards the surface, the uppermost strongly sclerenchymatic. *Chlorobiont* of *cf. Myrmecia* cells, irregularly globose to ellipsoid, 6–15 × 7–15 µm, chlorobiont layer 30–60 µm thick. *Medulla* 40–60 µm thick. *Hypocortex* lacking. *Cephalodia* brown, common, located directly on the prothallus/hypothallus or on the the squamules, 0·3–1·5 mm wide, globose to irregularly pulvinate. *Cyanobiont Nostoc,* cells bluish green, irregularly subglobose or ellipsoid, 3·5–7 × 4–8 µm, in 15–30 µm large, indistinct glomeruli, without visible chain structures.

Apothecia sessile to subsessile, laminal, 0·5–2·5 mm wide. *Discs* reddish brown to chestnut-brown, mostly flat. *Thalline excipulum* 0·1–0·3 mm wide on mature apothecia when seen from above, regularly crenulate-striate, with anatomy as in the squamules. *Epithecium* light brown, *c.* 10 µm thick. *Hymenium* colourless, but strongly IKI + blue, *c.* 70–80 µm thick. *Asci* clavate, *c.* 20 × 70–80 µm, with 8 ascospores and a long and narrow, sometimes apically widening tube-like structure, IKI + blue, sometimes laminated, in addition to a more diffuse large apical IKI+ structure, most often also a small IKI+ external apical cap. *Proper ascospores* hyaline, non-septate, short-ellipsoid, 12–20 × 8–12 µm; *perispores* 18–29 × 9–13 µm, ellipsoid, even, and with two broad apical extensions. *Paraphyses* weakly septate, mostly unbranched, apices 2–3 µm wide, weakly swollen. *Hypothecium* light brown, *c.* 70 µm thick, IKI−.

Chemistry. Usnic acid (major/minor) and up to 13 unidentified terpenoids, at present not known from any other lichens and with one to four of them always present in major quantities.

Etymology. Named after its yellow colour due to usnic acid.

Key to the *Xanthopsoroma* species

1 Soredia present; apothecia not uncommon, but less than 1 mm wide and mostly with a thalline central plug, proper ascospores 15–20 µm long and perispores with nodulose apical extensions. Contains '*X. soccatum* terpenoids', one in major quantities . . . . . **X. soccatum**

Esorediate; apothecia very common, up to 2 mm wide and without thalline central plugs. Proper spore/perispore shapes and chemistry variable 2

2(1) Apothecia with thick margins, short-ellipsoid proper ascospores (12–16 µm) and perispores mostly with large, truncate apical extensions. Contains '*X. contextum* terpenoids', normally three in major quantities . . . . . **X. contextum**

Deviations from one or more of these four characters . . . . . **X. cf. contextum**

Xanthopsoroma contextum (Stirt.) Elvebakk comb. nov.

Basionym: *Psoroma contextum* Stirt., *Proc. Phil. Soc. Glasgow* **10:** 294 (1877); type: New Zealand, near Wellington, 1974, *J. Buchanan* 46/74 (BM— lectotype!; WELT— isolectotype!).

(Figs 6A, 7 & 8A)

Characters as in the description of the genus, except for the following:

Chlorobiont squamules 150–180 µm thick, appressed to the substratum, in peripheral parts up to 2 mm wide, in central parts strongly imbricate, yellowish green, turning more yellow after decades of storage. *Epicortex* 40–60 µm thick. *Chlorobiont* 7–15 × 6–12 µm, chlorobiont layer 50–60 µm thick. *Medulla* 50–60 µm thick.

Apothecia common, subsessile, laminal, 0·5–2·5 mm wide. *Thalline excipulum* 0·2–0·3 mm wide on mature apothecia when seen from above. *Asci* long and narrow, sometimes apically widening, IKI + blue, tube-like structure. *Proper ascospores* short-ellipsoid, 12–16 × 8–10·5 µm; *perispores* 18–25 × 9–11·5 µm, with two 3–4 µm broad apical extensions, either short (*c.* 1 µm) or enlarged to regularly truncate extensions, 4–5 µm long, occasionally deviating, even vesicular.

Chemistry. Usnic acid (minor) and three to eight unidentified terpenoids (Fig. 9), at present not known from any other lichen. '*X. contextum* terpenoids 1–3' are constantly present, mostly in major quantities, '*X. contextum* terpenoid 4' is present in only 20–30% of the specimens sampled, but in major quantity, '*X. contextum* terpenoids 5–8' appear mostly in trace quantities, and their presence appears to be depending mainly on the concentrations of the TLC samples.

Additional selected specimens examined. **Argentina:** *Tierra del Fuego*: Lago Fagnano, E end, Cabezera Lago, 1940, *R. Santesson* 7927 (S).—**Chile:** *Archipiélago de Juan Fernández*: Isla Robinson Crusoe, Miradór de Selkirk, 33° 38′ S, 78° 51′ W, 2006, *A. Elvebakk* 06:338 (TROM). *IX Región de la Araucanía*: Parque Nacional Nahuelbuta, Pehuenco, 37° 36′ S, 72° 48′ W, 2008, *A. Elvebakk* 08: 323B (TROM). *XI Región Aysén*: 3 km N of the village Río Cisnes, 44° 41′ S, 72° 15′ W, 2006, *A. Elvebakk* 06:469 (TROM); Valle Explotadores, 10 km W of Punta Río Tranquilo, 46° 37′ S, 72° 51′ W, 2007, *A. Elvebakk* 07:051 (TROM); 38 km N of Bahía Murta along the road, W of Laguna Cofré, 46° 11′ S. 72° 45′ W, 2007, *A. Elvebakk* 07:314 (TROM); Puerto Aysén, 1940, *R. Santesson* 4347 (S). *XII Región de Magallanes*: Laguna el Parrillar, 40 km SW of Punta Arenas, 53° 22′ S, 71° 07′ W, 1999, *A. Elvebakk* 99:739 (TROM); Punta Arenas, Tres Puentes, 1940, *R. Santesson* 8078 (S); Isla Riesco, Mina Elena, 1940, *R. Santesson* 2051, 7818 (S).—**Australia:** *Tasmania*: Pelion Plains, *c.* 1 km SW of Pelion Hut, saxicolous, 41° 50′ S, 146° 02′ E, 1992, *G. Kantvilas* 215/92 (HO); Grass Tree Hill, 42° 47′ S, 147° 22′ E, 1981, *G. Kantvilas* 706/81 (HO); Mt. Sprent, 42° 48′ S, 145° 58′ E, 1987, *G. Kantvilas* s. n. (HO 12450); Lake Skinner Track, 42° 56′ S, 146° 42′ E, 1980, *G. Kantvilas* 236/80 (HO); South Sister, near summit, 41° 32′ S, 148° 10′E, 2004, *J. A. Elix* 28583 & *G. Kantvilas* (CANB).—**New Zealand:** *South Island*: Golden Bay Co., Cobb, Fenella Hut, 41° 03′ S, 172° 31′ E, 1975–1985, *J. K. Bartlett* s. n. (AK 178956); Buller Co., Mount Arthur, 1975–1985, J. K. *Bartlett* s.n. (AK 197994).

Xanthopsoroma soccatum (R. Br. ex Crombie) Elvebakk comb. nov.

Basionym: *Psoroma soccatum* R. Br. ex Cromb., *Journ. Linn. Soc., Bot.* **17:** 398 (1879); type: Tasmania, Table Mt. [= Mt. Wellington], *R. Brown*, *Iter austr. 502* (BM— lectotype).

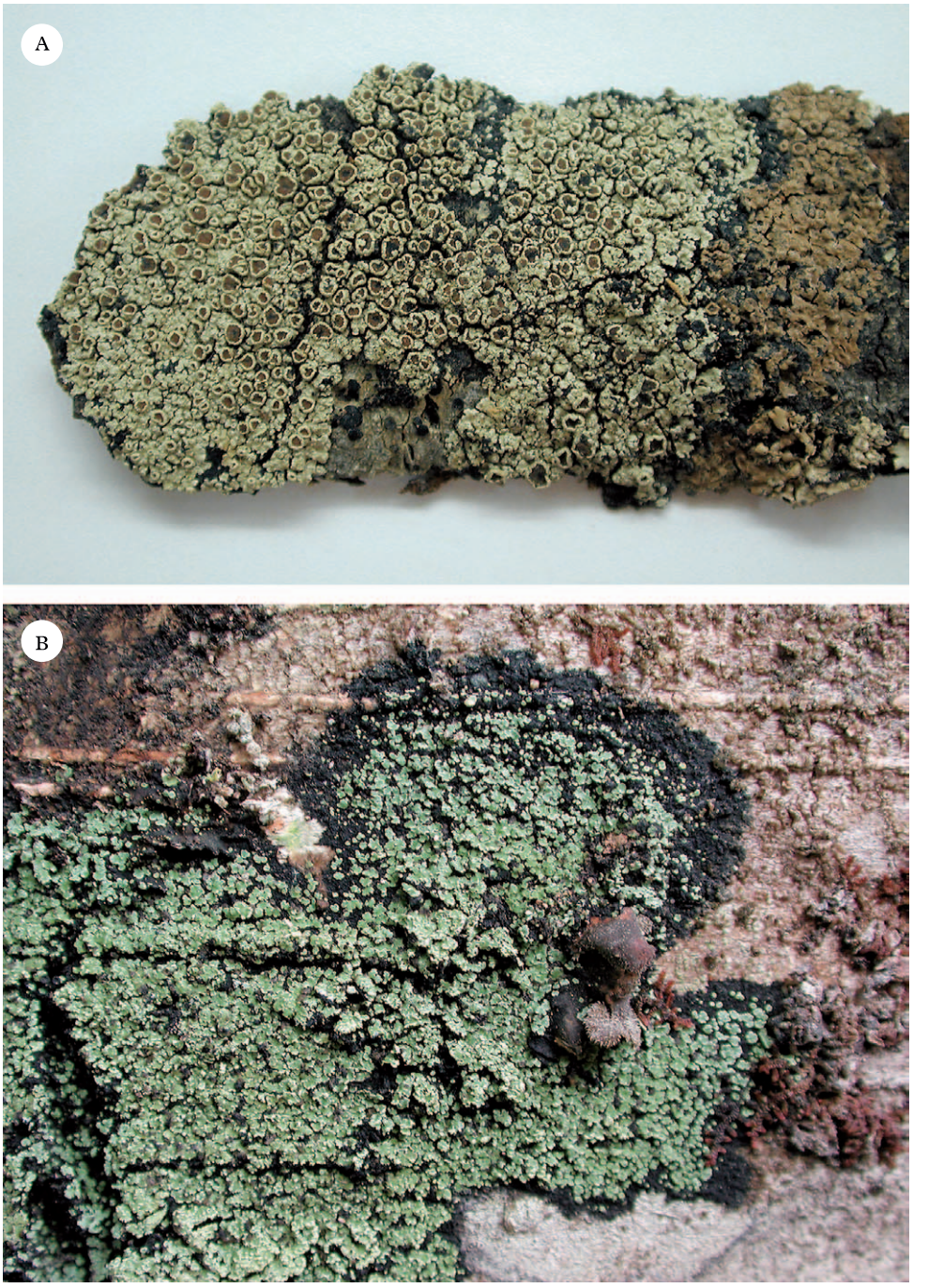

FIG. 6. *Xanthopsoroma* species. A, *X. contextum* (WELT— isolectotype); B, *X. soccatum*.

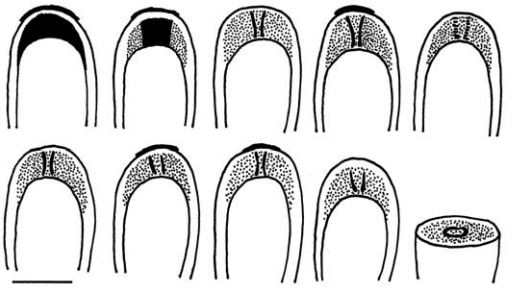

FIG. 7. *Xanthopsoroma*, IKI+ ascus apical structures (two upper left samples with high IKI concentrations). Scale = 10 μm.

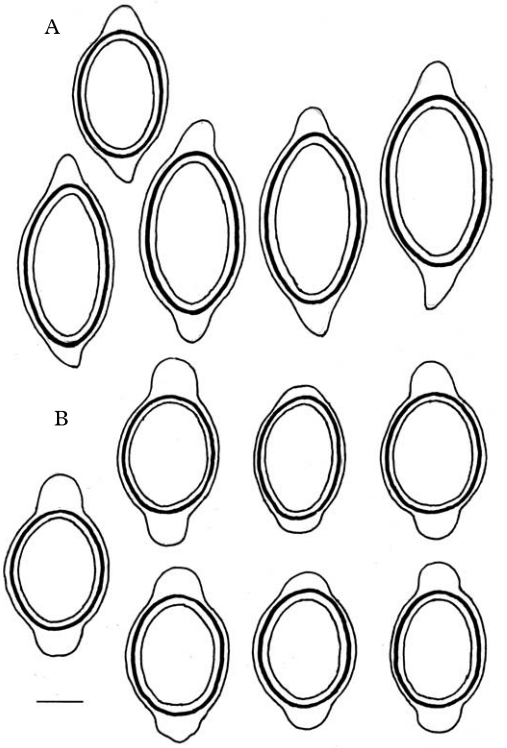

FIG. 8. *Xanthopsoroma*, ascospores. A, *X. soccatum*; B, *X. contextum*. Scale = 5 μm.

(Figs. 6B, 7, 8B & 9)

Characters as in the description of the genus, except for the following:

Chlorobiont squamules 120–40 μm thick, appressed to the substratum, in peripheral parts up to 1 mm wide, in central parts strongly imbricate, yellowish green, turning ochraceous after decades of storage. *Soralia* common, labriform to irregular and laminal, of soredia *c*. 0·05 mm. *Epicortex* 40–50 μm thick. *Chlorobiont* 7–13 × 6–12 μm, chlorobiont layer 30–40 μm thick. *Medulla* 40–50 μm thick.

Apothecia uncommon, sessile to subsessile, laminal, 0·5–1·0 mm wide, often with a central, thalline plug. *Thalline excipulum* 0·1–0·2 mm wide on mature apothecia when seen from above. *Asci* with a long and narrow, tube-like IKI+ blue structure, only occasionally apically widening. *Proper ascospores* 15–20 × 8–12 μm; *perispores* 22–29 × 9–13 μm, with two large, irregular and mostly nodulose apical extensions, 2–4 × 2–6 μm.

Chemistry. Usnic acid (major), one to five unidentified '*X. soccatum* terpenoids', 1 in minor to major quantities, the others mostly as traces (Fig. 9). The terpenoids are presently not known from any other species.

Additional selected specimens examined. **Argentina:** *Prov. Neuquén*: Nahuel Huapi National Park, between Puerto Blest and Laguna los Cantaros, 41° 01′ S, 71° 50′ W, 1989, *M. Wedin* 1831 (UPS).—**Chile:** *Archipiélago de Juan Fernández*: Isla Robinson Crusoe, 1·5 km W of San Juan Bautista along the path to Miradór de Selkirk, 33° 38′ S, 78° 51′ W, 2006, *A. Elvebakk* 06:230; 06:273; 06:284A (TROM). *XIV Región de los Ríos*: Lago Panguipulli, Volcán Choshuenco, 1940, *R. Santesson* 3938A (S); Lago Riñihue, Enco, 1940, *R. Santesson* 7617 (S). *XI Región Aysén*: Puerto Aysén, 1940, *R. Santesson* 4350 (S); 15 km S of Lago Torres NE of Puerto Aysén, 44° 57′ S, 72° 10′ W, 2006, *A. Elvebakk* 06:429 (TROM). *XII Región de Magallanes*: Península Brunswick, 10–15 km S of Fuerte Bulnes, near Río San Pedro, 53° 36′ S, 70° 58′ W, 1998, *A. Elvebakk* 98:270B, *J. W. Bjerke & E. Domínguez* (TROM).—**Australia:** *Victoria*: Errinundra National Park, Rainforest Walk, 300 m S of Cobb Hill, 37° 19′ S, 148° 50′ E, 2008, *A. Elvebakk* 08:122; 08:130; 08:146 (TROM); Bemm River Scenic Reserve, 45 km E of Orborst, 37° 38′ S, 148° 53′ W, 2008, *A. Elvebakk* 08:085B (TROM). *Tasmania*. Arve Valley, west of Geeveston, Keough's Creek Forest Walk, 43° 09′ S, 146° 48′ E, 2008, *A. Elvebakk* 08:219B (TROM); Cradle Mountain-Lake St. Clair National Park, S end of Lake Clair, Cynthia Bay, 42° 07′ S, 140° 10′ E, 2008, *A. Elvebakk* 08:171 (TROM).—**New Zealand:** *North Island*: Wellington, Central Volcanic Plateau, N side of Mt. Ruapehu, 1·5 km S of Whakapapa Village, 39° 12′ S, 175° 32′ E, 2002, *A. Elvebakk* 02:402 (TROM). *South Island*: Canterbury, *c*. 10 km N of Lake Wanaka, 1 km N of Makarora, near Pipson Creek, 44° 14′ S, 169° 15′ E, 2002, *A. Elvebakk* 02:434 (TROM).

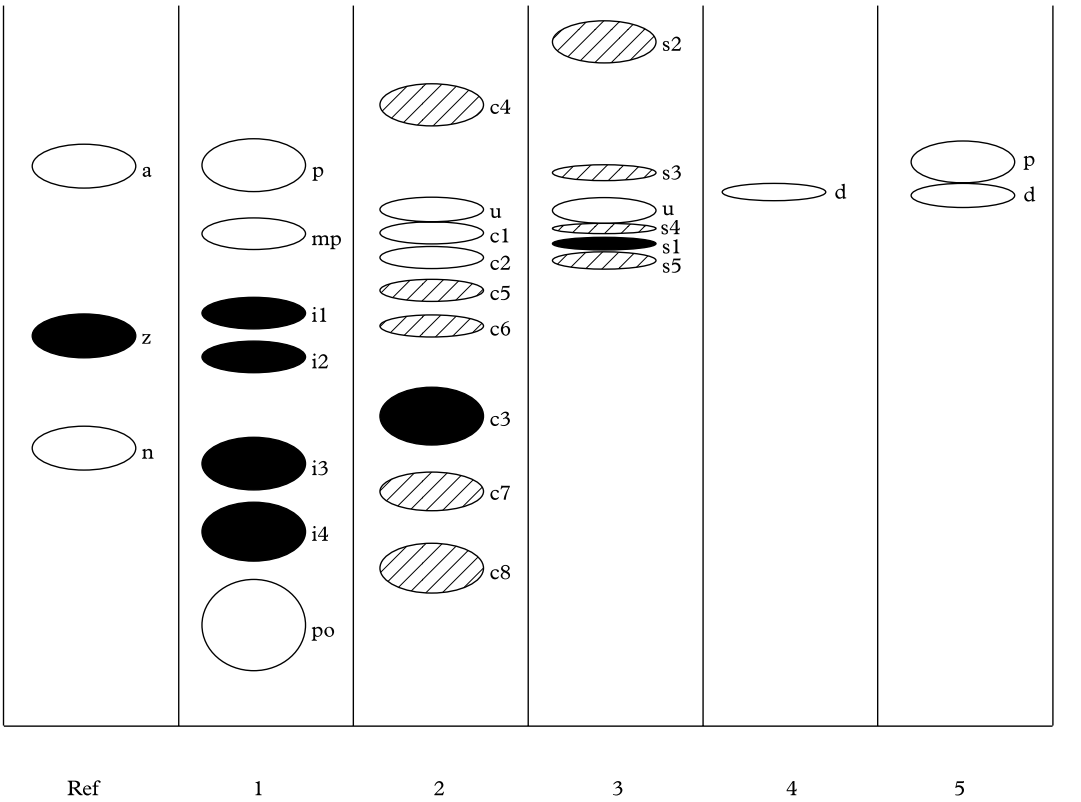

FIG. 9. Chromatogram showing TLC-detectable compounds in solvent C in 1) *Pannaria isidiosa* Elvebakk & Elix, 2) *Xanthopsoroma contextum*, 3) *X. soccatum*, 4) *Phyllopsora* sp., and 5) *Pannaria pallida* (Nyl.) Hue. Only major compounds are included among the latter, p = pannarin, mp = methylplacodiolic acid, i1–i4 = '*Pannaria isidiosa* terpenoids 1–4', po = porphyrilic acid, c1–c8 = '*Xanthopsoroma contextum* terpenoids 1–8', u = usnic acid, s1–s5 = '*Xanthopsoroma soccatum* terpenoids 1–5', d = dechloropannarin. References: a = atranorin, z = zeorin, n = norstictc acid. Terpenoids occurring in major quantities are shown in black.

Discussion of *Xanthopsoroma* species

In both phylograms, *X. contextum* and *X. soccatum* appear as distinct clades. The latter species is very homogeneous in all its characters studied. Apart from its soredia it differs from *X. contextum* in having smaller and thinner squamules, smaller and fewer apothecia mostly with thalline central plugs, narrower thalline excipuli, long-ellipsoid spores, narrower and often nodulose apical perispore extensions, and different terpenoids. There are no significant differences between specimens from South America and New Zealand/Australia. The species are so different that *X. soccatum* should not be considered a sorediate counterpart of *X. contextum* as stated, for example by Kantvilas & Jarman (1999), who provide good illustrations of both species. Here, and in all other recent literature, *X. contextum* has been interpreted as *Psoroma pholidotoides* (Nyl.) Trev. The holotype of the latter, H-NYL 30773!, however, defines a very different species with pannarin as its major secondary compound. This analysis was unambiguous, and in accordance with a previous and unpublished analysis by J. A. Elix.

The chemistry of these species has also been misunderstood. Jørgensen & Galloway (1992) cited *X. soccatum* to contain dechloropannarin and usnic acid, a report repeated by later studies. Dechloropannarin was first reported for *X. contextum* (as *Psoroma*

reticulatum) by Quilhot *et al.* (1989), who reported three chemical strains, with usnic acid and various combinations of three other substances, probably a result of mixed samples. This is the source of the frequently cited chemosyndrome of 'vicanicin, ± pannarin, ±leprolomin and ±usnic acid' for the species previously interpreted as *P. pholidotoides*. Dechloropannarin was described by Elix *et al.* (1982) from the lichen *Psoroma caesium* Müll. Arg., now *Phyllopsora* sp. (Jørgensen 2003). A sample of '*Psoroma caesium*' was obtained from J. A. Elix. Dechloropannarin is instead a compound closely associated with pannarin, in TLC overlapping with pannarin in solvent A, but slightly below pannarin in solvent C and becoming brownish after storage, compared with pannarin. It appears to have been correctly reported from *Pannaria pallida* by Quilhot *et al.* (1989), but reported as norpannarin from the same species by Passo & Calvelo (2004).

The unidentified terpenoids reported here for the two species are unknown from *Pannariaceae*, and not known to the present authors to be identical to terpenoids from any other lichen species. They are all different from those of *Pannaria isidiosa* Elvebakk & Elix, the only other *Pannariaceae* species, except *Pannaria durietzii* (P. James & Henssen) Elvebakk & D. J. Galloway, with terpenoids present as major compounds (Fig. 9). They are also different from zeorin, reported from the latter species, but probably erroneously reported from *Pannariaceae*, as stated by Elvebakk & Elix (2006).

The chemosyndromes of *X. soccatum* and *X. contextum* are very different. The former was found to be very homogeneous in its chemistry as well as in other characters. *Xanthopsoroma contextum*, on the other hand, was found to be much more complex. A number of specimens are in close accordance with the type, and are referred to in the description and included as cited specimens. They are also widely distributed from southern South America, to New Zealand and Australia, where also *X. soccatum* is a common species. Among the deviating specimens in the *X. contextum* complex, several primarily fertile specimens, including NK 78 and 79 in the phylograms, had *X. soccatum* chemistry so that we searched for a primarily fertile counterpart species of the latter. However, characters derived from a limited number of specimens did not form any clear pattern. Five specimens among these deviating types are represented in the phylograms, where they were clustered with *contextum* and not with *soccatum*. These deviating samples are at present referred to as *X.* cf. *contextum*, and further studies based on a larger selection of samples are needed.

The genus *Xanthopsoroma* is very distinct in several characters, and its primarily fertile species can be expected to be evolutionarily old, allowing for some variation which is not yet understood.

General Discussion

The genera

The trees presented in Figs 1 & 2 confirm the previously published pattern of a major subdivision into a *Pannaria* s. lat. and a *Psoroma* s. lat. clade. In the *Pannaria* clade, the bipartite species were separated from the tripartite ones, as in the study by Passo *et al.* (2008). In Fig. 2, the squamulose and foliose tripartite species are in different positions. However, this tree is based on ITS only, the number of added sequences is low, and relationships within the *Pannaria* s. lat. clade are outside the scope of the present study.

Psorophorus is morphologically a distinct genus, with its small and very thin, corticolous squamules. They maintain a distinct green colour much longer than other similar species such as the pannarin-containing species such as *P. implexum*, which soon become more uniformly grey after storage. *Psorophorus* has a very massive chlorobiont layer, a poorly specialized epicortex, with very thin-walled cells. Together with the lack of secondary compounds this probably accounts for the maintenance of the green algal colour in the lichen. Thus the colour of the genus is surprisingly similar to the usnic acid genus *Xanthopsoroma*. It should also be

noted that there is no abrupt change of colour in these lichens when water is added to dead specimens as in *Xanthopsoroma* and tripartite *Pannaria* species with a TLC-detectable chemistry (see Elvebakk 2007). However, there is a slow colour change to olive-brown after decades of storage.

The cephalodia are very characteristic, often larger than the chlorobiont squamules, and always develop directly on the hypothallus/prothallus, although this is less evident in central parts of the thallus where the squamules are confluent. In *Psorophorus pholidotus* in particular, cephalodia are very conspicuous and often represent 20–40 % of total cover of squamules on the hypothallus. The lack of secondary cortical compounds and specialized cortical cells probably represents an adaptation to humid areas. The unusual high biomass of cephalodia might be an adaptation to low light intensities. The habitat conditions for both species known to us are in old-growth forests of high rainfall areas in Chilean Patagonia and in Isla Robinson Crusoe. In the latter area, *P. pholidotus* was collected in a protected, moist area (Plazoleta del Yunque, at 250–300 m altitude, with a strong preference for trunks of *Drimys confertifolia*) and on a light-exposed, but much fog-affected pass (Miradór de Selkirk, 540–570 m altitude, on thin twigs of shrubs), which would be in agreement with the species' obvious requirement for humidity on the mainland.

Chemically, the genus is TLC negative, similar to most species in *Psoroma* s. str., and different from most other small-squamulose, tripartite *Pannariaceae* species. It differs from the former in many characters, such as its strictly corticolous habitat, thin and strongly adpressed squamules, shape of cephalodia, lack of melanins, and microscopically by its small tube-like IKI+ ascus apical structure. However, *Psorophorus* is a sister group to *Psoroma* in the phylogram, and the closeness of these two groups illustrates the taxonomic importance of chemistry in psoromoid lichens.

Xanthopsoroma is now shown to be a very distinct genus. Its general appearance differs from *Psoroma* s. str. in being corticolous with adpressed squamules on a very distinct hypothallus, and from *Psorophorus* by having much thicker squamules and a differentiated cortical cell structure. Its unique chemistry and perispore structure separate it from all other genera in *Pannariaceae*. Except for its usnic acid colour it looks quite similar to other corticolous squamulose species, such as *Psoroma implexum* Stirt., now transferred to *Pannaria* by Passo *et al.* (2008).

Apical amyloid structures have long been considered an important character in *Pannariaceae* (Keuck 1977; Jørgensen 1978), but have rarely been studied in detail, although Keuck (1977) included an illustration (fig. 180, of '*Psoroma reticulatum*'), most probably referring to *X. contextum*. The present study shows that both *Psorophorus* and *Xanthopsoroma* have long, IKI+ apical tubes without the basal and apical internal sheets mostly seen in the asci of *Psoroma hypnorum*. In addition, *Xanthopsoroma* also has a general, but less IKI+ active tholus, which can hide the tube structure when studied in high IKI concentrations. Most asci of *Xanthopsoroma* also have an external apical IKI+ sheath.

These findings confirm several previous statements that chemistry and ascus IKI structures are important synapomorphies in the phylogeny of *Pannariaceae* lichens. Our phylogenetic analyses have also indicated that a stable classification is obtained only after a reasonable number of samples are represented in each clade. This is valid also for single species defined as study targets, and is an aspect mostly lacking from previous phylogenetic studies involving *Pannariaceae*.

Psoroma s. str. species

Psoroma s. str. was introduced primarily as a reference to the phylogenetic study of the species now positioned in *Psorophorus* and *Xanthopsoroma*. The selection of material included several collections of each of six terricolous/muscicolous *Psoroma* s. str. species. The genus is monophyletic in both our trees. For comparison, *Psoroma hypnorum* itself has been studied, and found to differ from the two new genera in its terricolous/

muscicolous habitat, inconspicuous hypothallus, thick squamules not densely adpressed to the substratum, presence of brownish melanins, perispores with more robust verrucae, and large, verruciform apical extensions. The IKI+ apical ascus structure in *P. hypnorum* was called a 'manubrium' by Jørgensen (1978), a properly chosen name meaning 'handle'. More detailed illustrations here confirm this structure which is clearly different from those in the two new genera.

Most of these characters are valid also for the remaining *Psoroma* s. str. species included in this study, although detailed studies on IKI + apical structures have not yet been carried out, and perispore structures also need to be more carefully compared. The *Psoroma* s. str. clade also shows a dichotomy, with the four sequences of *P. tenue* and *P. cinnamomeum* forming a very well-supported subclade. This was unexpected, as there are no evident synapomorphies characterizing these two clades separately, as opposed to characters of each of the species involved. This phylogenetic analysis reveals that these groups obviously have had a long-lasting separate evolutionary history, and we believe this is the primary reason for the rather low bootstrap support of the present *Psoroma* s. str. clade. This will be explored more thoroughly in a future study involving many more planned sequences.

Although nested within the *Psoroma* s. str. clade in Fig. 2, *Psoroma aphthosum* is a deviant species. It is corticolous, has pannarin instead of melanins and has a different squamule structure. Further detailed studies are needed before its taxonomic position can be confirmed.

After the present treatment above, 26 of the species listed within *Psoroma* by Jørgensen (2003) still remain. A final definition of *Psoroma* s. str. after the segregation of *Psorophorus* and *Xanthopsoroma* also depends on future studies of additional primarily corticolous species, particularly from New Zealand and south-eastern Australia, and a group of foliose species centred in tropical South East Asia. *Psoroma* also needs to be defined vs. the poorly understood genus *Santessoniella*. With its biatorine apothecium and amyloid apical ascus ring/tube, it was originally thought to be most closely related to the bipartite cyanolichen genus *Parmeliella* (Henssen 1997). However, the tube structure could instead reveal a relationship with *Psoroma*, and *Santessoniella* species. Some of them should be studied further to investigate any potential homologies of their tube structures with *Psoroma* cephalodia, a hypothesis first put forward by Ekman & Jørgensen (2002).

The study by Passo *et al.* (2008) did not resolve the relationship between the studied species in the *Psoroma hypnorum* group. In the present study *P. fruticulosum* forms a well-defined group of three closely related samples. *Psoroma buchananii* also forms a well-defined clade of closely related samples. In Fig. 2 the *Passo* 39 sample of *P. hypnorum* is found to be genetically almost identical to one of the present samples of *P. buchananii* and it is believed to belong to the latter species. *Psoroma paleaceum* also forms a well-defined clade, including the sample *Passo* 22 shown in Fig. 2.

Two Chilean samples of *Psoroma cinnamomeum* and two Antarctic samples of *Psoroma tenue* formed a very well-defined subclade within the *Psoroma* s. str. group. This is a phylogenetic position in need of further studies, which is also the case with *P. hypnorum* itself, which appears heterogeneous in the present phylograms.

The authors are indebted to the curators of AK, BM, CANB, H, HO, PC-MONT, TROM, S, UV, W, and WELT for loans and for the opportunity to study at their herbaria, to CONAF for collection permits in Chile, to the Dept. of Sustainability and Environment in Victoria and the Dept. of Primary Industries, Water and Environment, Tasmania, for collection permits in Australia, and to J. A. Elix, Australian National University, for a reference sample. The first author also appreciated Jack Elix's hospitality and '5 o'clock beer discussions' when in Australia, and nice company in the field together with him, P. McCarthy and G. Kantvilas, as well as hospitality shown by D. J. Galloway, Landcare Research, and W. Quilhot and C. Rubio, Universidad de Valparaíso, during visits to New Zealand and Chile, respectively. Per P. Aspaas, Tromsø University Library, kindly translated the diagnoses into Latin. This research was partly supported by the Korea Polar Research Institute (Grants PE08050 and PE09130).

References

Calvelo, S. & Liberatore, S. (2002) Catálogo de los líquenes de la Argentina. *Kurtziana* **29** (1)**:** 1–174.

Culberson, C. F. (1972) Improved conditions and new data for the identifications of lichen products by a standardized thin layer chromatography method. *Journal of Chromatography* **72:** 113–125.

Ekman, S. & Jørgensen, P. M. (2002) Towards a molecular phylogeny for the lichen family *Pannariaceae*. *Canadian Journal of Botany* **80:** 625–634.

Elix, J.A., Lajide, L. & Galloway, D. J. (1982) Metabolites from the lichen genus *Psoroma*. *Australian Journal of Chemistry* **35:** 2325–2333.

Elvebakk, A. (2007) The panaustral lichen *Pannaria sphinctrina* (Mont.) Tuck. and the related new species *P. lobulifera* from New Caledonia. *Cryptogamie, Mycologie* **28:** 225–235.

Elvebakk, A. & Bjerke, J. W. (2005) *Pannaria isabellina* (Vain.) comb. nov., a remarkable lichen species from Chile. *Lichenologist* **37:** 47–54.

Elvebakk, A. & Elix, J. A. (2006) *Pannaria isidiosa*, a new Australian lichen with a new chemosyndrome. *Lichenologist* **38:** 557–563.

Elvebakk, A. & Galloway, D. J. (2003) Notes on the heterogeneous genus *Psoroma* s. lat. in New Zealand. *Australasian Lichenology* **53:** 4–9.

Follman, G. (1965) Catálogo de los líquenes de Chile. III. Thelotrematales y Cyanophiliales. *Revista Universitaria* (*Universidad Católica de Chile*) **49:** 17–65.

Gardes, M. & Bruns, T. D. (1993) ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2:** 113–118.

Gay, C. (1852) *Historia fisica y politica de Chile segun documentos adquiridos en esta Republica durante doce años de residencia en ella y publicada bajo los auspicious del supremo gobierno. Botanica, Tomo octavo*. Chile & Paris: Museo de Historia Natural de Santiago.

Grassi, M. M. (1950) Contribución al catálogo de líquenes argentinos, I. *Lilloa* **24:** 1–290.

Guindon, S. & Gascuel, O. (2003) A simple, fast and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* **52:** 696–704.

Hasegawa, M., Kishino, K. & Yano, T. (1985) Dating the human-species splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution* **22:** 160–174.

Hue, A. M. (1892) Lichenes exotici a professore W. Nylander descripti vel recogniti et in herbario Musei Parisiensis pro maxima parte asservati in ordine systematico dispositi sunt. *Nouvelles Archives du Muséum d'Histoire Naturelle de Paris, 3. Série* **4:** 103–210.

Hue, A. M. (1902) ['1901'] Causerie sur les *Pannaria*. *Bulletin de la Societé Botanique de France* **48:** XXXI–LXV.

Hue, A. M. (1906) Lichenes morphologice et anatomice disposuit. *Nouvelles Archives du Muséum d'Histoire Naturelle de Paris* **8:** 237–272.

Hue, A. M. (1908) Lichenes morphologice et anatomice, 1. *Nouvelles Archives du Muséum d'Histoire Naturelle de Paris* **10:** 169–224.

Jeon, Y. S., Chung, H., Park, S., Hur, I., Lee, J. H. & Chun, J. (2005) jPHYDIT: a JAVA-based integrated environment for molecular phylogeny of ribosomal RNA sequences. *Bioinformatics* **21:** 3171–3173.

Jørgensen, P. M. (1978) The lichen family *Pannariaceae* in Europe. *Opera Botanica* **45:** 1–123.

Jørgensen, P. M. (1999) Studies in the lichen family *Pannariaceae* VIII. Seven new parmelielloid lichens from New Zealand. *New Zealand Journal of Botany* **37:** 257–268.

Jørgensen, P. M. (2001) ['2000'] Survey of the lichen family *Pannariaceae* on the American continent, north of Mexico. *Bryologist* **103:** 670–704.

Jørgensen, P. M. (2003) Conspectus familiae *Pannariaceae* (Ascomycetes lichenosae). *Ilicifolia* **4:** 1–79.

Jørgensen, P. M. (2004) *Psoroma tenue* var. *boreale*, an overlooked, widespread, arctic-alpine lichen. *Graphis Scripta* **15:** 60–64.

Jørgensen, P. M. & Galloway, D. J. (1992) *Pannariaceae*. *Flora of Australia* **54:** 246–293.

Kantvilas, G. & Jarman, S. J. (1999) Lichens of rainforest in Tasmania and south-eastern Australia. *Flora of Australia Supplementary Series* **9:** 1–212.

Keuck, G. (1977) Ontogenetisch-systematische Studie über *Erioderma*. *Bibliotheca Lichenologica* **6:** 1–175.

Kimura, M. (1980) A simple method for estimating evolutionary rate of base substitution through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* **16:** 111–120.

Malme, G. O. A. (1925) Die Pannariazeen des Regnellschen Herbars. *Arkiv för Botanik* **20A** (3)**:** 1–23.

Montagne, C. (1835) Prodromus Floræ Fernandesianæ. Pars prima, sistens enumerationem plantarum cellularium quas in Insulá Juan Fernandez à Cl. Bertero collectas describe edique curavit. *Annales des Sciénces Naturelles, Botanique*, **4:** 86–90.

Nordin, A. (1997) Ascospore structures in *Physciaceae:* an ultrastructural study. *Symbolae Botanicae Upsalienses* **32** (1)**:** 195–208.

Nylander, W. (1855*a*) Additamentum in floram cryptogamicam chilensem, quo lichens præcipue saxicolas exponit. *Annales des Sciénces Naturelles, Botanique, Séries 4*, **3:** 145–187.

Nylander, W. (1855*b*) Südamerikanische Flechten, gesammelt durch W. Lechler, bestimmt durch Dr. W. Nylander. *Flora* **43:** 673–675.

Nylander, W. (1859) Dispositio Psoromatum et Pannariarum. *Annales des Sciences Naturelles, Botanique, Séries 12*, **4:** 293–295.

Nylander, W. (1863) *Synopsis methodica lichenum omnium hucusque cognitorum praemissa introductione lingua gallica tractata*. Parisiis: Fasc. II.

Orange, A., James, P. W. & White, F. J. (2001) *Microchemical Methods for the Identification of Lichens*. London: British Lichen Society.

Passo, A. & Calvelo, S. (2004) Taxonomic notes on *Pannaria pallida* from southern South America and New Zealand. *Mycotaxon* **90:** 355–365.

Passo, A. & Calvelo, S. (2006) New reports and combinations in the family *Pannariaceae* (*Lecanorales*, lichenized Ascomycota). *Lichenologist* **38:** 549–555.

Passo, A., Stenroos, S. & Calvelo, S. (2008) *Joergensenia*, a new genus to accommodate *Psoroma cephalodinum* (lichenized Ascomycota). *Mycological Research* **112:** 1465–1474.

Quilhot, W., Piovano, M., Arancibia, H., Garbarino, J. A. & Gambaro, V. (1989) Studies on Chilean lichens, XII. Chemotaxonomy of the genus *Psoroma*. *Journal of Natural Products* **52:** 191–192.

Räsänen, V. (1932) Zur Kenntnis der Flechtenflora Feuerlands sowie der Prov. de Magallanes, Prov. de Chiloë und Prov. de Ñuble in Chile auf Grund des von H. Roivainen gesammelten Materiales. *Annales Botanici Societatis Zoologicae-Botanicae Fennicae 'Vanamo'* **2**, I–VI: 1–65.

Rehner, S. A. & Samuels, G. J. (1994) Taxonomy and phylogeny of *Gliocladium* analysed from nuclear large subunit ribosomal DNA sequences. *Mycological Research* **98:** 625–634.

Swofford, D.L. (2002) *PAUP*. Phylogenetic Analysis using Parsimony* (** and Other Methods*). *Version 4*. Sunderland, Massachusetts: Sinauer Associates.

Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F. & Higgins, D. G. (1997) The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **24:** 4876–4882.

Timdal, E. & Tønsberg, T. (2006) *Psoroma paleaceum* comb. nov. the only hairy *Psoroma* in northern Europe. *Graphis Scripta* **17:** 54–57.

Vilgalys, R. & Hester, M. (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* **172:** 4238–4246.

White, T. J., Bruns, T.D., Lee, S. B. & Taylor, J. W. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In *PCR Protocols: A Guide to Methods and Applications* (M. A. Innis, D. H. Gelfand, J. J. Sninsky & T. J. White eds): 315–322. San Diego: Academic Press.

Zahlbruckner, A. (1917) Botanische Ergebnisse der schwedischen Expedition nach Patagonien und dem Feuerlande 1907–1909. VI. Die Flechten. *Kungliga Svenska Vetenskapsakademiens Handlingar* **57** (6): 1–62.

Zahlbruckner, A. 1924. 11. Die Flechten der Juan Fernandez-Inseln. In *The Natural History of Juan Fernandez and Easter Island. Vol. II Botany* (C. Skottsberg, ed.), **11:** 315–408.

Accepted for publication 07 *January* 2010