Extended phylogeny and a revised generic classification of the Pannariaceae (Peltigerales, Ascomycota)

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Abstract: We estimated phylogeny in the lichen-forming ascomycete family Pannariaceae. We specifically modelled spatial (across-site) heterogeneity in nucleotide frequencies, as models not incorporating this heterogeneity were found to be inadequate for our data. Model adequacy was measured here as the ability of the model to reconstruct nucleotide diversity per site in the original sequence data. A potential non-orthologue in the internal transcribed spacer region (*ITS*) of *Degelia plumbea* was observed. We propose a revised generic classification for the Pannariaceae, accepting 30 genera, based on our phylogeny, previously published phylogenies, as well as morphological and chemical data available. Four genera are established as new: *Austroparmeliella* (for the '*Parmeliella*' *lacerata* group), *Nebularia* (for the '*Parmeliella*' *incrassata* group), *Nevesia* (for '*Fuscopannaria*' *sampaiana*), and *Pectenia* (for the '*Degelia*' *plumbea* group). Two genera are reduced to synonymy, *Moelleropsis* (included in *Fuscopannaria*) and *Santessoniella* (included in *Psoroma*). *Lepidocollema,* described as monotypic, is expanded to include 23 species, most of which have been treated

in the '*Parmeliella*' *mariana* group. *Homothecium* and *Leightoniella*, previously treated in the Collemataceae, are referred here to the Pannariaceae. We propose 42 new species-level combinations in the newly described and re-circumscribed genera mentioned above as well as in *Leciophysma* and *Psoroma*.

Key words: Collemataceae, lichen taxonomy, model selection, model adequacy

Introduction

Peltigerales comprises one out of nine named orders in the most species-rich class among the ascomycetes, the Lecanoromycetes (Schoch *et al*. 2009), and incorporates the majority of lichen-forming fungi with cyanobacteria as their photosynthesising symbiotic partner. The peltigeralean lichens play an important role in the terrestrial nitrogen cycle of many ecosystems through the fixation of atmospheric nitrogen (Cleveland *et al*. 1999; Belnap 2003). Current classifications of the Peltigerales include ten families (Wedin *et al*. 2007; Spribille & Muggia 2013), four of which include *c*. 90% of the total species number of the order, i.e., Lobariaceae, Pannariaceae, Collemataceae, and Peltigeraceae (Kirk *et al*. 2008). Several recent contributions have significantly increased knowledge about broad phylogenetic relationships in the Peltigerales (Wedin *et al*. 2007, 2009; Otálora *et al*. 2010; Muggia *et al*. 2011; Spribille & Muggia 2013).

Current estimates indicate that the Pannariaceae is the second most species-rich family of the Peltigerales and includes more than 300 known species (Kirk *et al*. 2008). In its original description (Tuckerman 1872), however, the Pannariaceae included only two genera, *Pannaria* and *Heppia*. It was not until the treatment by Zahlbruckner (1926) that the familial circumscription was stabilised and came to include large and well-known genera like

Psoroma and *Parmeliella*, which are still treated in the Pannariaceae. Zahlbruckner included altogether eleven genera, although he excluded *Heppia*. Some genera included by Zahlbruckner, i.e., *Hydrothyrea*, *Massalongia*, *Placynthium* and *Coccocarpia*, have later been excluded from the Pannariaceae (see, e.g., Wedin *et al*. 2007, 2009). Jørgensen (1978, 1994) pointed out that Zahlbruckner's generic classification had paid too much attention to photobiont (green algal or cyanobacterial) and presence or absence of a thalline margin in the apothecia. In the survey by Henssen & Jahns (1973), only four genera were included in the Pannariaceae: *Lepidocollema, Pannaria, Parmeliella*, and *Psoroma*. A preliminary single-gene phylogeny of the family (Ekman & Jørgensen 2002) confirmed that *Protopannaria* is distinct from *Pannaria* (in which it had previously been included), that *Pannaria* included a mixture of species with a green algal and cyanobacterial photobiont, and excluded the *Fuscopannaria leucophaea* group, later described as *Vahliella* (Jørgensen 2008), from the Pannariaceae. Continued revision of familial and generic boundaries led Jørgensen (2003) to recognise altogether 17 genera, although some with doubt. Later investigations demonstrated that all studied genera with non-septate ascospores (*Leciophysma*, *Physma*, *Ramalodium*, and *Staurolemma*), traditionally referred to the Collemataceae because of their gelatinous thallus, should be transferred to the Pannariaceae (Wedin *et al*. 2009; Otálora *et al*. 2010; Muggia *et al*. 2011). In addition, *Vahliella* was shown to belong in a family of its own, Vahliellaceae (Wedin *e*t *al*. 2009, 2011), whereas species with a *Scytonema* photobiont previously treated in *Polychidium* belong in a genus of Pannariaceae, *Leptogidium* (Muggia *et al*. 2011).

Despite previous efforts, phylogenetic relationships within the Pannariaceae remain insufficiently known. Our aim was to estimate phylogenetic relationships in the Pannariaceae based on an expanded sampling of taxa and provide a revised taxonomic overview of the family in light of the phylogenetic estimate, previously phylogenetic estimates, as well as morphological data.

Material and methods

Taxonomy and nomenclature

We studied the type species of most described genera in the Pannariaceae, located in the herbaria cited in the taxonomical section below. The morphology and anatomy of the specimens were investigated, and chemistry was investigated by thin-layer chromatography (Culberson & Kristinsson 1970).

Taxon selection for molecular studies

We selected representatives of all genera included in the Pannariaceae as circumscribed by Jørgensen (2003), Wedin *et al*. (2009), Muggia *et al*. (2011), and Spribille & Muggia (2013) except *Kroswia* (Jørgensen & Gjerde 2012), *Leptogidium* (Muggia *et al*. 2011), *Psoromidium* (Galloway & James 1985), and *Steineropsis* (Spribille *et al*. 2010; Spribille & Muggia 2013). We were unable to obtain fresh enough material of *Lepidocollema* and *Psoromidium*, whereas repeated attempts to generate PCR products from *Kroswia* were unsuccessful. *Leptogidium* and *Steineropsis* were not included because they were recognised as members of the Pannariaceae only after the initiation of this study (Muggia *et al*. 2011; Spribille & Muggia 2013). Altogether, the data matrix included 110 ingroup terminals representing 88 species (Supplement Table S1). *Vahliella leucophaea*, a member of the Vahliellaceae (Wedin *et al*. 2011), was used as outgroup.

DNA extraction, PCR amplification and sequence editing

We obtained DNA sequences from three different genes, the largest subunit of the RNA polymerase II gene (*RPB1*), the internal transcribed spacer (*ITS*) region (including *ITS1*, *5.8S*, and *ITS2*) of the nuclear ribosomal RNA gene, and the small subunit of the mitochondrial ribosomal RNA gene (*mrSSU*). Laboratory methods follow Lindblom & Ekman (2005), Ekman *et al*. (2008), Wedin *et al*. (2009), and Ekman & Blaalid (2011).

Alignment of ITS

The *ITS1* region was assumed to start immediately after GATCATTA pattern at the end of the small subunit of the nuclear ribosomal RNA gene region. The *ITS2* region was assumed to end after the 9th nucleotide preceding the TCGGATCA pattern at the beginning of the large subunit of the nuclear ribosomal RNA gene region. Borders between *ITS1* and *5.8S* and between *5.8S* and *ITS2* were defined using the Rfam *5.8S* seed alignment (Gardner *et al*. 2009). A preliminary alignment was created using the G-INS-I algorithm of MAFFT version 6.820 (Katoh & Toh 2008). The *ITS* region was subsequently split into separate data sets. The *5.8S* region was considered unambiguously and finally aligned, whereas the *ITS1* and *ITS2* regions were prepared for downstream structural alignment by stripping all gaps introduced by the preliminary alignment procedure. The two gene regions were subsequently aligned separately using three different structural aligners, viz. Murlet version 0.1 (Kiryu *et al*. 2007), CentroidAlign version 1.0 (Hamada *et al*. 2009.), and MAFFT with the X-INS-i algorithm

using MXSCARNA pairwise structural alignments and Contrafold base-pairing probabilities (Katoh & Toh 2008). The three structural alignments (for each gene region) were combined into a single alignment for each gene region using T-Coffee version 8.93 (Notredame *et al*. 2000). Subsequently, we filtered out ambiguously aligned regions as well as sites with a nucleotide in a single terminal and a gap in all other terminals. We defined ambiguous alignment as sites with a local consistency score (described by Notredame & Abergel 2003) less than 5. Scores from 5 to 9 (the highest) are, according to the documentation, considered to be correctly aligned with a probability exceeding 90%, given the underlying separate alignments. In other words, we kept alignment for which the three structural aligners generally agreed and excluded the rest.

Alignment of mrSSU

We downloaded the structural euascomycete mitochondrial 16S rRNA gene reference alignment from the Comparative RNA Web Site (http://www.rna.ccbb.utexas.edu; Cannone *et al*. 2002). We added our unaligned sequences to this profile using the L-INS-i algorithm of MAFFT and subsequently removed the profile and resulting gap-only columns. Ambiguously aligned sites were removed using Aliscore version 1.0 (Misof & Misof 2009). All possible pairs of taxa were used to infer the consensus profile. The window size was set to 4 and gaps were treated as ambiguities.

Alignment of RPB1

Initial alignment was performed using the L-INS-i algorithm of MAFFT. Introns were identified and excised in accordance with the GenBank records submitted by James *et al*. (2006). Finally, we trimmed the alignment to start with the first complete codon after the first intron reported by James *et al*. (2006). The end of the alignment was trimmed to end after a third codon position and to keep the amount of missing data in the final alignment position below 50%.

Selection of partitioning scheme

The data was tentatively partitioned into seven initial subsets: *ITS1*, *5.8S*, *ITS2*, *mrSSU*, and *RPB1* first, second, and third codon positions, respectively. These subsets were subsequently input to PartitionFinder version 1.0.1 (Lanfear *et al*. 2012) for an exhaustive search for the best-fitting partitioning scheme. We used the Bayesian Information Criterion (BIC) to select among models and partitioning schemes. We only considered proportional models ("branchlengths = linked") across subsets (Pupko *et al*. 2002). The BIC has been shown to more accurately identify the generating model than the commonly used Akaike Information Criterion (AIC), assuming that the true generating model is included in the set of candidate models (Darriba *et al*. 2012).

Model selection

Although PartitionFinder reports a selected model for each of the partitions suggested, we performed a more thorough model selection from among the GTR family of likelihood

models, including rate heterogeneity across sites and a proportion of invariable sites, on each of the final five subsets suggested by PartitionFinder. Model selection was performed using the Perl script MrAIC version 1.4.4 (Nylander 2004) in combination with PhyML version 20110919 (Guindon *et al*. 2010). As before, the BIC, with alignment length taken as sample size, was used to select among models. We included the number of branches in the number of free model parameters but we did not add an extra parameter for the topology. We selected among a reduced set of models with one, two, or six substitution rate categories, i.e. the ones available in frequently used software like MrBayes version 3 (Ronquist & Huelsenbeck 2003). We consistently used six discrete gamma categories for modelling rate heterogeneity across sites. We modified MrAIC to improve PhyML search intensity by performing both NNI and SPR branch swapping and choose the best outcome (the default is to perform only NNI branch swapping).

Model adequacy assessment

We assessed model adequacy (Goldman 1993; Bollback 2002), i.e. the adequacy of the selected model to generate patterns similar to the observed sequence data. Model adequacy was assessed with PhyloBayes using posterior predictive simulation from the GTR+Γ and F81+Γ+CAT models for each of the five subsets in the phylogenetic analysis. Simulations were performed across a random subset of 1000 trees drawn from the posterior distribution. We used the mean number of states per site ('site diversity') as test statistic. Reported posterior predictive probabilities correspond to the fraction of times that the value from the posterior simulation exceeded the value observed from the data. Note that these are not probabilities in the classical sense, but rather describe the position of the test statistic derived

from the observed data relative to the simulated data. The match to the model is perfect when the observed data fall in the centre of the simulated data, i.e. when p is close to 0.5. Both extremely high and extremely low values of p signal poor adequacy of the model to reproduce the observed data. We considered p<=0.025 or p>=0.975 (i.e. the extreme 5%) as a significant departure from the model. We deliberately chose to avoid the unconstrained (multinomial) likelihood as test statistic (e.g., Bollback 2002), as all current implementations, unlike site diversity, require that all sites with gaps be excluded.

Phylogenetic analyses

PhyloBayes version 3.3b (Lartillot *et al*. 2009) was used to infer phylogeny under a baseline GTR+Γ model as well as under a F81+Γ+CAT and GTR+Γ+CAT model, using data from each of the five subsets separately as well as the concatenated data. Gamma distributed rate heterogeneity across sites was approximated as six discrete categories in all cases. Note that PhyloBayes does not implement a proportion of invariable sites. For concatenated data, we explored models with and without proportional branch lengths across subsets suggested by PartitionFinder. Under the CAT model (Lartillot & Philippe 2004) substitution rates are constant across sites and trees, whereas state frequencies are treated as a Dirichlet process with an infinite number of mixtures across sites, unobserved states at each site being united into a single state (Lartillot *et al*. 2007). We used default priors, except that the prior on branch lengths was set to an exponential with a mean seeded by an exponential hyperprior with mean 0.1. We chose an exponential prior because empirical data suggest that true branch lengths are often exponentially distributed (Venditti *et al*. 2010). Single-subset analyses were performed with three parallel runs, which were set to terminate automatically when the

effective sample size of all model parameters exceeded 100 and the maximum discrepancy between runs of the likelihood and all diagnosed parameters descended below 0.1, discrepancy being measured as twice the difference in mean divided by the sum of standard deviations. The burn-in was set to a fifth of the chain length and is fixed by the software. In the end, however, we accepted only runs as converged if, in addition, the discrepancy of all parameters in the second half of the run was below 0.3. Concatenated analyses were performed in a similar manner, except that the three runs, for reasons of computational time, were treated as separate processes for a fixed number of cycles, 60000. We subsequently applied the same convergence criteria as in the analyses of the individual partitions, except that we discarded the first half of the runs as burn-in and used every 10th tree from the second half of the runs to calculate a majority-rule consensus tree.

We also used MrBayes version 3.2.1 (Ronquist & Huelsenbeck 2003; Ronquist *et al*. 2012) to infer phylogenies under a model with five partitions, each subset with the model favoured by MrAIC. Gamma distributed rate heterogeneity across sites was approximated with six categories. Prior distributions included treating all tree topologies as equally likely, and (when applicable) a uniform (0.001, 200) distribution for the gamma shape parameter, a uniform (0, 1) distribution for the proportion of invariable sites, a (1, 1, 1, 1, 1, 1) Dirichlet for the rate matrix, independent beta (1, 1) distributions for the transition and transversion rates, and a (1, 1, 1, 1) Dirichlet for the state frequencies. The number of discrete categories used to approximate the gamma distribution was set to six in all analyses. We assumed an exponentially distributed branch length prior. The exponential distribution was parameterised with an empirical Bayes' approach (Ekman & Blaalid 2011), whereby the inverted branch length average calculated from a phylogeny generated with PhyML 3.0 online (Guindon *et al*. 2005, 2010) was used as the exponential distribution rate parameter (d). This phylogeny was generated with a heuristic search involving NNI and SPR branch swapping from 10 random

and one BIONJ tree under a GTR+I+Γ model. Three parallel Markov chain Monte Carlo (MCMC) runs were performed, each with four parallel chains and the temperature increment parameter set to 0.10 (Altekar *et al*. 2004). The appropriate degree of heating was determined by observing swap rates between chains in preliminary runs. Every 1000th tree was sampled. Analyses were diagnosed for convergence every 10^6 generations in the last 50% of the tree sample and automatically halted when convergence was reached. Convergence was defined as an average standard deviation of splits (with frequency 0.1) between runs below 0.01. Finally, the potential scale reduction factor (PSRF) was monitored manually, and we only accepted runs with PSRF values smaller than 1.1 for all model parameters and all bipartitions.

Incongruence between the three genes (not the five partitions) was assessed by identifying conflicts between majority-rule consensus trees obtained by (1) maximum likelihood (ML) bootstrap analyses with PhyML 3.0 online and (2) Bayesian MCMC using PhyloBayes under a F81+Γ+CAT model. Each bootstrap analysis included 1000 bootstrap replicates and was performed under a GTR+I+Γ model. PhyloBayes analyses were performed in the same way as other analyses with this software described above. Majority-rule consensus trees were subsequently passed to Compat.py (Kauff & Lutzoni 2002) for identification of conflicts. Tests were performed between all three pairs of genes. The cut-off for conflict identification was set to 0.7 in the ML analysis and 0.95 in the Bayesian analysis.

Branch attachment frequencies were calculated for selected taxa using Phyutility version 2.2.5 (Smith & Dunn 2008).

Marginal likelihoods of the data were calculated with Tracer version 1.5 (Rambaut & Drummond 2009) using importance sampling as suggested by Newton & Raftery (1994) and modified by Suchard *et al*. (2003).

Results

Resources

The concatenated data, individual gene data used for assessing congruence, as well as all majority-rule consensus trees estimated from these data (including branch lengths and support values) are permanently filed in the TreeBASE repository (http://www.treebase.org) under study number 14978.

Partitioning and model selection

The selection of a partitioning scheme using PartitionFinder on the concatenated data indicated a preference for five subsets, viz. *ITS1+ITS2*, *5.8S*, *mrSSU*, *RPB1* first and second codon positions, and *RPB1* third codon positions. The following models were selected by MrAIC under the Bayesian Information Criterion: HKY+Γ for the *ITS1+ITS2*, K80+I+Γ for the *5.8S*, HKY+I+Γ for the *mrSSU*, GTR+Γ for the *RPB1* 1st+2nd positions, and HKY+I+Γ for the *RPB1* 3rd positions. Descriptive statistics for the five subsets as well as the concatenated data are found in Supplement Table S2.

Gene tree incongruence

We identified two conflicts between gene trees. The very different placement of *Degelia plumbea* caused a deep conflict between the *ITS* on the one hand, and the *mrSSU* and *RPB1*

trees on the other hand in the ML bootstrap consensus but not in the Bayesian consensus. However, branch attachment frequencies reveal that in the Bayesian posterior tree sample obtained from *ITS* data, the three samples of *Degelia plumbea* cluster together with 100% posterior probability, and as sister group to *Staurolemma omphalarioides* with 98% posterior probability, a relationship that does not at all make sense from a morphological perspective. In the *mrSSU* and *RPB1* trees, *D. plumbea* clusters, as expected from morphology, with *D. atlantica* and *D. cyanoloma*. Because of this deep incongruence, we excluded *ITS* sequences from *Degelia plumbea* from the concatenated data. The second conflict, supported by both the ML and Bayesian consensus tree, occurred between the *ITS* and *RPB1* and concerned the branching order among five closely related species of *Pannaria*. We did not exclude any taxa on account of this shallow incongruence.

Model adequacy

A GTR+Γ model was deemed significantly inadequate ($p = 1.000$) in case of the *mrSSU* and the *RPB1* third codon positions, with poor performance also in the subsets consisting of *ITS1* and *ITS2* ($p = 0.970$), 5.8S ($p = 0.844$), and the *RPB1* first and second codon positions ($p = 0.943$). The F81+Γ+CAT model was not rejected for any of the five subsets ($0.118 \leq p \leq 0.711$).

Phylogeny from concatenated data

The ln marginal likelihoods calculated from the posterior samples produced by MrBayes (under a partitioned model, each subset with model selected by MrAIC) and PhyloBayes (under a F81+Γ+CAT model) were -19754.560 and -18454.879, respectively. The superiority of the F81+Γ+CAT model in this case, despite its very simple underlying substitution rate model, is not caused by differences in priors or the MCMC machinery across software, as analyses of each of the five subsets with MrBayes and PhyloBayes under a single GTR+Γ model produce closely matching marginal likelihoods (results not shown). The median posterior number of nucleotide frequency categories ("profiles") in the CAT model was 42. Apparently, there are substantial differences in nucleotide frequencies across our sequence data, leading to vastly different local instantaneous rates of substitution. We take the results from the F81+Γ+CAT model as our phylogenetic estimate, because this model clearly outperforms standard GTR family models with respect to model adequacy and likelihood. A majority-rule consensus tree with all compatible groups obtained with PhyloBayes under a F81+Γ+CAT model without subset-specific rate multipliers is shown in Fig. 1. Convergence statistics for this analysis translated to MrBayes standards (by feeding reformatted tree samples to 'sumt' of MrBayes) correspond to an average standard deviation of splits = 0.004 and a maximum topology PSRF = 1.003. We experienced severe convergence issues under the GTR+Γ+CAT (with and without subset-specific rate multipliers) as well as the F81+Γ+CAT with subset-specific rate multipliers despite very long runs, leading us to discard the results from these analyses.

Discussion

Model adequacy, robustness, and branch support

Spuriously high branch support in Bayesian phylogenetics sometimes reported (summarised by Alfaro & Holder 2006) can have two explanations, disregarding MCMC machinery failure: misspecified priors and/or under-parameterised models (Yang 2006: 178-179). We safeguarded against the bias from a misspecified prior on branch lengths by use of a hyperprior (in PhyloBayes) or an empirical Bayes prior (in MrBayes) (Kolaczkowski & Thornton 2007; Ekman & Blaalid 2011). Bayesian branch support estimates seem to be particularly sensitive to model under-parameterisation (Buckley 2002; Lemmon & Moriarty 2004; Huelsenbeck & Rannala 2004; Brown & Lemmon 2007). Therefore, we conducted an assessment of model adequacy in an attempt to identify a model that was capable of reproducing patterns of the observed data. We found that ordinary GTR family models, including rate heterogeneity across sites, were inadequate as long as spatial heterogeneity in nucleotide frequency, and consequently local differences in the instantaneous rates of substitution, were not included in the model. A model incorporating this process, in this case CAT (Lartillot & Philippe 2004), was found to be adequate for all our data subsets as measured by nucleotide site diversity. Branch support generated from an adequate model is unlikely to be overestimated. Indeed, average support for internal branches in the consensus tree estimated by MrBayes (not shown here but included in the TreeBASE submission) was on average 2.1% higher than the corresponding tree obtained with PhyloBayes (87.7 vs. 85.6%) and three branches in the MrBayes consensus had distinctly higher support to the point where it would affect conclusions drawn from the analysis.

Gene tree conflicts

The ML phylogeny based on the *ITS* data conflicted with the corresponding *mrSSU* and *RPB1* ML phylogenies regarding the position of *Degelia plumbea*, which is represented by three different samples, all from western Norway. During the course of this investigation, identical *ITS* sequences were recovered from several more specimens, also from Norway, that are not reported here. The lack of apparent conflict regarding the position of *D. plumbea* between the Bayesian gene consensus trees is ostensibly caused by poor backbone support in the *ITS* consensus tree. The poor support is not caused by rogue behaviour of *D. plumbea*, as branch attachment frequencies indicate that *D. plumbea* clusters on a long branch as sister group to *Staurolemma* with 98% posterior probability. This association cannot be reconciled with morphology. In the *mrSSU* and *RPB1* Bayesian as well as ML phylogenies, *D. plumbea* clusters, as expected from morphology, with *D. atlantica* and *D. cyanoloma*.

The *ITS* sequences we have recovered from *Degelia plumbea* may ultimately prove to be non-orthologous. The same potential non-orthologue was captured by Ekman & Jørgensen (2001) and fell outside the Pannariaceae in their phylogeny. Interestingly, what seems to be the orthologue was recently reported by Otálora *et al*. (2013), who used different PCR primers and sampled from a different geographic area, southern and central Spain. There are, however, no reported cases of ascomycetes containing a non-orthologous rDNA sequence that was transformed extensively by processes not mastered by current phylogenetic likelihood models. We do not claim the *ITS* sequences observed in *D. plumbea* to be the first such case, because crucial experimental evidence of intragenomic variation is still lacking. However, our observations call for further scrutiny.

A second gene tree conflict involved the branching order between *Pannaria rubiginosa*, *P. rubiginella*, *P. tavaresii*, *P. subfusca*, and *P. hookeri* in the *ITS* and *RPB1* trees. These taxa form a group of closely related species (Jørgensen 1978). Shallow conflicts like these may represent incomplete lineage sorting (a.k.a. deep coalescence). In such instances,

concatenation of data from several genes has been shown to be a poor method for estimating the species tree (Edwards *et al*. 2007; Kubatko & Degnan 2007). Unlike the case of *Degelia plumbea*, pointing out a single culprit offending congruence is not possible. We did not proceed to exclude any data from the concatenated analysis, as we were primarily interested in inferring boundaries and relationships at the genus level. We note, however, that inferred relationships from the concatenated data between taxa involved in this conflict must be interpreted with caution.

Overview of the Pannariaceae

The Pannariaceae, as currently circumscribed, has previously been shown to be monophyletic (Wedin & Wiklund 2004; Wedin *et al*. 2007, 2009; Muggia *et al*. 2011; Spribille *et al*. 2013), and falls into two major clades (Clade 1 and 2 in Fig. 1), which to some extent coincide with the formation of a secondarily developed margin of thalline origin in the apothecia of the second clade and the corresponding absence of such a margin in the first clade. There are several exceptions to this rule, however, *Joergensenia* having a well developed secondary thalline margin, as well as species scattered in the second clade lacking thalline margin, mainly in gelatinous taxa with a cyanobacterial photobiont. Clade 1 includes *Parmeliella*, *Degelia*, *Degeliella*, *Siphulastrum*, *Joergensenia*, *Leioderma*, and *Erioderma*. According to Muggia *et al*. (2011), the genus *Leptogidium*, not included in our study, also belongs here. Clade 2 consists of three subclades (2a-c) and *Xanthospsoroma*. Clade 2a includes *Fuscopannaria sensu lato* (incl. *Moelleropsis*), *Leciophysma*, *Protopannaria* and some species referred to *Santessoniella*. The recently described *Steineropsis* (Spribille *et al*. 2010), although not included in our study, also belongs here (Spribille & Muggia 2013). Clade 2b

contains *Pannaria*, *Ramalodium*, and *Staurolemma*, and Clade 2c includes *Psoroma sensu lato*, *Fuscoderma*, *Austrella*, *Santessoniella*, *Psorophorus*, and *Physma*. The genus *Xanthopsoroma* falls outside these clades in our phylogeny. Support for its monophyly is very weak, but support for branches on either side of the genus is high, indicating that *Xanthopsoroma*, as currently understood, is either monophyletic or a paraphyletic grade.

Generic taxonomy and biogeography

We recognise altogether 30 genera in the Pannariaceae, although some provisionally. The two largest genera, *Pannaria* and *Lepidocollema*, are mostly tropical with some extensions through the subtropical region into warm temperate regions. The highest number of genera is found in the Southern Hemispheric region, particularly in South America, possibly reflecting a long and complex biogeographic history in that part of the world. Three genera are confined to the Northern Hemisphere, two in the Atlantic-Mediterranean part of Europe (*Nevesia* and *Pectenia*) and one in North America (*Fuscopannaria*). *Fuscopannaria* is the largest genus of the family in the temperate zone and is particularly species-rich in the North Pacific region, although a few species extend into the Southern Hemisphere. *Psoroma sensu stricto* is genuinely bipolar, although far more species-rich in the Southern Hemisphere than elsewhere.

Synopsis of genera in the Pannariaceae

In this section, we briefly treat all genera currently accepted by us, the delimitation of which mostly emerge from the phylogenetic estimate (Fig. 1) but also on grounds of previous

phylogenetic estimates as well as morphological and chemical data. We include also genera that were not part of the phylogeny, which we refer to the family based on other than phylogenetic evidence. Finally, we present an identification key to the accepted genera.

Genera in bold font are accepted genera. A star in front of the name indicates that no member of the genus was included in our phylogeny. Genera in regular font are names for genera that are considered here as synonyms and should be abandoned. We provide full descriptions of newly established genera.

Austrella P. M. Jørg. (Fig. 5C) was described by Jørgensen (2004) for the type species *A. arachnoidea* and *A. brunnea*, which are characterised by the formation of apothecia from non-lichenised fungal hyphae, a thick subhymenium of densely packed tissue, and the lack of an apical apparatus in the asci. We provisionally retain the genus as originally conceived, although we note that *Austrella* has an uncertain position within Clade 2c.

Austroparmeliella (P. M. Jørg.) P. M. Jørg. *comb. nov.*

Parmeliella sect. *Austroparmeliella* P. M. Jørg., Bibl. Lich. 88: 244 (2004)

Generitype: *A. lacerata* (P. M. Jørg.) P. M. Jørg. (Fig. 5C)

MycoBank No.: MB

Thallus bluish grey, composed of squamules that form a lace-like crust. Squamules usually deeply incised, 2–3 mm wide, up to 75 µm thick; upper cortex 10–15 µm thick, cellular; medulla up to 50 µm thick, of loosely arranged, intricate hyphae enclosing clusters of *Nostoc*; lower cortex of a single cell-layer or lacking in parts of the thallus.

Apothecia frequent, often grouped, *c.* 1 mm diam., becoming convex at maturity, with red-brown disc surrounded by pale rim; proper exciple paraplectenchymatous, 30–50 µm

wide. *Subhymenium* colourless, flat, 100–150 µm thick, of intricately interwoven hyphae. *Hymenium* 100–150 µm µm high, I+ deep blue. *Asci* cylindrical, with apical amyloid ring-structure, 8-spored; ascospores colourless with smooth wall, broadly ellipsoid, non-septate.

Pycnidia not observed.

Chemistry: No lichen substances (Jørgensen 2004).

Notes: This is a genus of small, Southern Hemispheric *Parmeliella*-like species with finely divided squamules, often with cortex also on the lower surface (in one case the lobes are cylindrical with surrounding cortex, see Jørgensen 2004). A further difference from *Parmeliella sensu stricto* is the narrow, flat, colourless subhymenium, as opposed to the often lentil-shaped, brownish subhymenium in *Parmeliella*. Our phylogeny suggests a sister-group relationship with *Psorophorus*, the members of which differ in the hemiamyloid hymenia and in forming thalline apothecial margins. Five species of *Austroparmeliella* are recognised here, the four species treated by Jørgensen (2004) and '*Santessoniella*' *elongata* (Henssen 1997). The latter, although not known to produce apothecia, is transferred here to *Austroparmeliella* on account of the presence of a lower cortex.

Degelia Arv. & D. J. Galloway (Fig. 2A) was originally described to accommodate coccocarpioid, Southern Hemispheric species with apothecia similar to *Parmeliella* (Arvidsson & Galloway 1981), but with different asci (without an apical amyloid tube). Jørgensen & James (1990) added the three species of the Northern Hemispheric '*Parmeliella*' *plumbea* group known at the time (*D. plumbea, D. atlantica,* and *D. ligulata*), and later Blom & Lindblom (2009) added one more species, *Degelia cyanoloma*. A separate section, *Amphiloma* P. M. Jørg. & P. James, with *D. plumbea* as its type species, was established for this group of species (Jørgensen & James 1990). The members of sect. *Amphiloma* possess a *Nostoc* photobiont, whereas the remainder of the genus is lichenised with *Scytonema*. A third

section, *Frigidae* P. M. Jørg., was described by Jørgensen (2004) for three Subantarctic species with a thick paraplectenchymatous upper cortex and a poorly developed secondary thalline corona. The type species of this section is *D. subcincinnata* (Nyl.) P. M. Jørg.

Our phylogeny (Fig. 1) indicates that *Degelia* as currently understood is non-monophyletic and that the monophyletic section *Amphiloma* should be recognised as a separate genus. Therefore, we introduce the new name *Pectenia* for this section (see below).

Degelia sect. *Frigidae* was not represented in our phylogeny. However, a member of this section, *D. symptychia* (Tuck.) P. M. Jørg., was represented in the phylogeny of Spribille & Muggia (2013) and was shown to belong in *Steinera* in the Koerberiaceae. Unfortunately, sequence data is currently lacking for the type species, *D. subcincinnata*, which is why we refrain from further taxonomic and nomenclatural changes at the moment.

In *Degelia sensu stricto*, there may be a problem with heterogeneity in what has been treated as *D. gayana*, the type species, unless this species-level non-monophyly is caused by incomplete lineage sorting or another (undetected) case of non-orthology (Fig. 1).

Degeliella P. M. Jørg. (Fig. 2C) was described by Jørgensen (2004) to accommodate *D. rosulata* (P. M. Jørg. & D. J. Galloway) P. M. Jørg., the type species, and *D. versicolor* (Hook. f. & Taylor) P. M. Jørg. (Jørgensen 2004). Morphologically, it was separated from *Degelia* on account of the non-amyloid hymenium and ascus, a feature shared by the closely related genera *Siphulastrum* and *Leioderma* (Galloway and Jørgensen 1987; Jørgensen 1998). *D. rosulata* possesses a cyanobacterial photobiont and smooth ascospores, whereas *D. versicolor* has a green algal primary photobiont and warted ascospores. In our phylogeny, the type species *D. rosulata* forms a monophyletic group with fair support (0.94 posterior probability) together with *Siphulastrum* and *Leioderma*. *D. versicolor* (Fig. 7E) is unlikely to

be monophyletic together with the type species and may deserve generic recognition (see *Psoromaria*).

Erioderma Fée (Fig. 2H) includes more than 30 species. The genus has a complex chemistry (Jørgensen & Arvidsson 2002) and is recognised by an ascomatal ontogeny unique to the family (Keuck 1977).

Fuscoderma (D. J. Galloway & P. M. Jørg.) P. M. Jørg. & D. J. Galloway (Fig. 5B) is a genus of five known species, two of which are represented in our phylogeny. They form a monophyletic group and is obviously distantly related to *Leioderma*, under which it was originally placed as a subgenus (Galloway & Jørgensen 1987). *Fuscoderma* belongs in Clade 2c, where it is the sister of the Andean genus *Nebularia* (see below). *Fuscoderma* is recognised by squamulose to subfoliose, heteromerous thalli with a *Nostoc* photobiont and brownish tomentum on the lower side, a non-amyloid hymenium (except the gel surrounding asci), lack of amyloid apical structures in the asci, and the production of vicanicin and/or norvicanicin (Jørgensen & Galloway 1989).

Fuscopannaria P. M. Jørg. (Fig. 3D) is a genus of *c*. 50 species that was separated from *Pannaria* on account of the hemiamyloid hymenium, asci with an amyloid apical ring-structure, and the production of fatty acids and terpenoids but not pannarin (Jørgensen 1978, 1994). In addition, most species are small-squamulose and form apothecia with a variably developed thalline margin, which can sometimes even be missing.

The majority of the species, including the type *F. leucosticta* (Tuck.) P. M. Jørg., forms a monophyletic group if *F. sampaiana* and *F. laceratula* are excluded. However, whereas *F. sampaiana* is included here in the newly described genus *Nevesia* (see below), we refrain

from a formal placement of *F. laceratula* awaitning improved taxon sampling. '*Fuscopannaria' laceratula* is set apart by its combination of secondary chemistry (atranorin) and a *Scytonema*-like photobiont (Jørgensen 2005a).

Moelleropsis nebulosa (Hoffm.) Gyeln. (Fig. 6A) is nested within *Fuscopannaria* as suggested already by Ekman & Jørgensen (2002), although scarce taxon sampling prevented them from definitively placing *Moelleropsis* in synonymy. This situation has unfortunate nomenclatural consequences, since *Moelleropsis* is an older name than *Fuscopannaria*. We retain the use of *Fuscopannaria*, including *Moelleropsis*, pending a final decision based on a proposal to conserve *Fuscopannaria* against *Moelleropsis* (Jørgensen *et al*. 2013).

Subgenus *Micropannaria* P. M. Jørg. was established to comprise *F. leucophaea* and related species (Jørgensen 1994) but was later described as a separate genus, *Vahliella* P. M. Jørg. (Jørgensen 2008) and is now placed in the currently monogeneric Vahliellaceae (Wedin *et al*. 2011; Spribille & Muggia 2013).

Homothecium A. Massal. is a genus of five small-sized species with gelatinous thallus from southern South America. The genus is morphologically and anatomically similar to *Ramalodium*, from which it differs mainly in the annular exciple (cupular in *Ramalodium*) and presence of an apical ring-structure in the ascus (none in *Ramalodium*) (Henssen 1965, 1979). Although currently referred to the Collemataceae (Lumbsch & Huhndorf 2010) and not included in our phylogeny, we provisionally treat *Homothecium* as another genus in the Pannariaceae with non-septate ascospores and gelatinous thallus.

Joergensenia Passo, S. Stenroos & Calvelo (Fig. 2E) was described by Passo *et al*. (2008) and appears in our phylogeny as the sister group to the morphologically and chemically very different *Erioderma*. *Joergensenia* (Fig. 1) is aberrant in being the only genus in Clade 1 with

a secondarily developed thalline margin in the apothecia, i.e., not an ontogenetically "true proper margin". The thalline "corona" in the apothecia of a few species of *Degelia* and *Degeliella* is, according to Henssen & James (1980), not an ordinary thalline margin. Furthermore, *Joergensenia* is characterised by its strongly amyloid cap-shaped plug in the ascus apex.

Kroswia P. M. Jørg. is a small genus (Jørgensen 2002) of three paleotropical species (Jørgensen & Gjerde 2012) that were formerly believed to be closely related to *Physma* (Swinscow & Krog 1988). However, the discovery of fertile material revealed characters in the hymenium suggesting a closer relation with *Fuscopannaria* (Jørgensen 2007). The globose, brown-pigmented ascospores are unique in the family.

Leciophysma Th. Fr. (Fig. 3C) was treated in detail by Henssen (1965). The genus is monophyletic if *Santessoniella saximontana* P. M. Jørg. & T. Sprib. is included. *Leciophysma* is distantly related to the type species of *Santessoniella*, *S. polychidioides*, which is morphologically similar and sometimes difficult to distinguish from *Leciophysma*.

Leioderma Nyl**.** (Fig 2G) forms a monophyletic group in a clade together with *Degeliella*, *Siphulastrum*, *Joergensenia*, and *Erioderma*. Morphologically, *Leioderma* is similar to *Erioderma*, from which it differs in lacking thallus chemistry. *Leioderma* as circumscribed here corresponds to *Leioderma* subgenus *Leioderma* of Galloway & Jørgensen (1987), whereas subgenus *Fuscoderma* corresponds to the genus *Fuscoderma* (see above).

Leightoniella Henssen, with its only known species *L. zeylanica* (Cromb. ex Leight.) Henssen, is known only from the type material, which was described in detail by Henssen

(1965). This genus has so far been classified in the Collemataceae (e.g., Lumbsch & Huhndorf 2010) and is characterised by the periclinally arranged hyphae in the exciple and the production of 'supporting tissue' along the thalline margin and thallus stalk (Henssen 1965). The thallus is gelatinous with cyanobacteria and ascospores are simple. Although not included in our phylogeny, we provisionally treat *Leightoniella* provisionally as another member of the Pannariaceae with gelatinous thallus and simple ascospores.

Lepidocollema Vain. was described by Vainio (1890) to accommodate a single gelatinous, homoiomerous *Parmeliella*-like species with a *Nostoc* photobiont, *L. carassense* Vain., which has been collected only once, in Brazil. Vainio also noted the striking similarity with the apothecia of *Parmeliella mariana* (as *Pannaria mariana*), although he acknowledged the difference in thallus anatomy, *P. mariana* being heteromerous (albeit also contaning *Nostoc*). Although material of the type species was unavailable to us, we accept the genus here for altogether 24 tropical species, including '*Parmeliella*' *stylophora* and '*P.*' *mariana* (Fig. 1). *Lepidocollema* as understood here is characterised by the formation of large, flat rosettes on a thick layer of rhizohyphae, the presence of a cellular thalline cortex, apothecia with a thalline margin, asci with a wide apical ring-structure, and thin-walled ascospores. The thallus is heteromerous in all species except the type species. The genus is sister to *Physma* (for differences see that genus). Most of the species have been treated in *Parmeliella* (e.g., Jørgensen & Galloway 1992), with which they are only distantly related.

****Leptogidium*** Nyl. was recently re-established for the type species *L. dendriscum* (Nyl.) Nyl. as well as *L. contortum* (Henssen) T. Sprib. & Muggia and *L. stipitatum* (Vězda & W. A. Weber) T. Sprib. & Muggia (Muggia *et al*. 2011). These species have traditionally been

treated in *Polychidium* (Henssen 1963), from which they are easily distinguished by the photobiont being *Scytonema* instead of *Nostoc*.

Moelleropsis Gyeln. (Fig. 6A), with its single species *M. nebulosa* (Hoffm.) Gyeln., is nested within *Fuscopannaria* and should be reduced into synonymy with that genus.

Nebularia P. M. Jørg. *gen. nov.* (Fig. 5A)

MycoBank No.: MB

Fuscodermi similis, sed thallo subtus sine tomento fusco et hymenio in iodo toto coerulescenti.

Generitype: *Nebularia incrassata* (P. M. Jørg.) P. M. Jørg.

Thallus brownish, composed of up to 3 mm wide squamules with up to 0.25 mm wide, thickened, digitate lobes; upper cortex prominent, cellular, up to 70 µm thick; medulla *c.* 150 µm thick, of intricately interwoven hyphae enclosing often densely packed clusters of *Nostoc*, individual cells 5–7 µm diam.

Apothecia up to 1.5 mm diam, reddish brown, flat, with paler, prominent rim; proper exciple paraplectenchymatous, up to 80 µm wide. *Subhymenium* poorly delimited, colourless with loosely interwoven hyphae, containing photobiont cells that penetrate marginally from below. *Hymenium* up to 150 µm thick, I+ deep blue. Asci cylindrical, with distinct apical amyloid tube, 8-spored; ascospores colourless with rugulose wall, globose to ellipsoid, non-septate.

Pycnidia not observed.

Chemistry: No lichen substances (Jørgensen 2000; Jørgensen & Palice 2010).

Etymology: From latin *nebula* (fog) and *–aris* (belonging to), as the species grows in 'selvas nubladas' (= foggy forests).

Nebularia is an Andean genus comprised of only two species, the type species *N. incrassata* and *N. psoromoides*. Both species were originally referred to *Parmeliella*, with which they are only distantly related according to our phylogeny. In our phylogeny, *Nebularia* belongs in Clade 2c, although support for relationships within that clade is poor. *Nebularia* is morphologically similar to *Fuscoderma* in the shiny apothecia with a prominent apothecial rim, and in photobiont cells penetrating into the subhymenium. The latter character is unique to the two genera within the family. However, the amyloid, I+ deep blue hymenium as well as the absence of tomentum on the lower surface sets *Nebularia* apart from *Fuscoderma*, which has a hemiamyloid hymenium and brown tomentum on the lower surface.

Nevesia P. M. Jørg., L. Lindblom, Wedin & S. Ekman *gen. nov*. (Fig.3A)

MycoBank No.: MB

Thallus crusto-squamulosus hypothallo distinco positus, castaneus cum sorediis granulatis eburneis sine acidis lichenosis. Apothecia matura et pycnidia ignota.

Generitype: *Nevesia sampaiana* (Tav.) P. M. Jørg., L. Lindblom, Wedin & S. Ekman

Thallus consisting of 2–3 mm wide, chestnut brown, appressed, up to 200 µm thick squamules; hypothallus well-developed, blue-black; upper cortex cellular, 50–60 µm thick; algal layer 50–70 µm thick, *Nostoc* cells 6–8 µm diam., in clusters; medulla 40–80 µm thick, of intricate, 3–4 µm wide hyphae, forming a lax plectenchyma, gradually merging into the hypothallus.

Apothecia with thalline margin, extremely rare, only known in an immature state without developed asci. Hymenium hemiamyloid.

Pycnidia not known.

Chemistry: No lichen substances (Jørgensen 1978).

Etymology: Named in honour of the Portuguese lichenologist Carlos das Neves Tavares (1914–1972), who first recognised *N. sampaiana* (as *Pannaria sampaiana*) at species level (Tavares 1950). He had a keen interest and substantial knowledge in the Pannariaceae, which he generously shared with PMJ when he started working on this group.

Notes: *Nevesia* is a monospecific genus. Originally included in *Pannaria*, its only species was later transferred to *Fuscopannaria* (Jørgensen 1994). It is not known with mature apothecia, and its former classification was essentially based on overall morphology, secondary chemistry, and the observation of a hemiamyloid reaction of the hymenium in immature apothecia (Jørgensen 1978, 1994). It differs from most species of *Fuscopannaria* in having a very well developed hypothallus, and in the chestnut coloured thallus lacking lichen substances. In our phylogeny, *Nevesia* is sister to a large group containing mainly *Leciophysma*, *Protopannaria*, and *Fuscopannaria*.

Pannaria Del. (Fig. 4C) is a genus of ca. 80 species, with *Pannaria rubiginosa* being the type species. The genus is recognised by a squamulose or foliose thallus, apothecia with a thalline margin, amyloid hymenium, asci without internal amyloid apical structures, and presence of pannarin and related substances (Jørgensen 1994, 2001a). Historically, *Pannaria* included squamulose species containing a *Nostoc* photobiont and apothecia with a thalline margin.

Most members of *Pannaria* included here form a monophyletic group, although a few may belong elsewhere, e.g., *P. isabellina*, *P. hispidula*, *P. orphnina*, and *P. dichroa*. *Pannaria isabellina* and *P. hispidula* form a poorly supported group with *Staurolemma* and

Ramalodium. Together with *Pannaria* s*ensu stricto* they form the strongly supported group we refer to here as Clade 2b. It is currently impossible to confirm or rule out the possibility that *P. isabellina* and *P. hispidula* belong in *Pannaria*. Also, *Pannaria dichroa* and *P. orphnina* appear to be currently misclassified and belong to Clade 2c (see discussion under *Psoroma*).

Our results support the notion that *Pannaria* also includes taxa with a green algal photobiont (in our phylogeny represented by *P. sphinctrina* and *P. microphyllizans*), previously treated in *Psoroma* (Jørgensen 2001a). There is no support for the recognition of subgenus *Lepidoleptogium* (A. L. Smith) P. M. Jørg., as the type species *L. montagnei* A. L. Smith is a member of the *Pannaria immixta* complex, which is nested inside *Pannaria sensu stricto* in our phylogeny.

Parmeliella Müll. Arg. (Fig. 2D) was originally established for squamulose members of the Pannariaceae with apothecia lacking thalline margin. In later treatments (e.g., Jørgensen 1978), it was restricted to include species with an amyloid apical ring-structure and lack of lichen substances in the thallus. Even after the separation of *Degelia* (see above), *Parmeliella* remained heterogeneous. Most species of *Parmeliella* form a monophyletic group, although *P. incrassata*, *P. lacerata*, *P. mariana,* and *P. stylophora* are obviously misclassified. However, *Parmeliella* can be retained as a monophyletic entity, including the type species *P. triptophylla* and the majority of species in the genus, if the tropical *Parmeliella mariana* group is excluded to *Lepidocollema,* and *P. lacerata* and *P. incrassata* are referred to the new genera *Austroparmeliella* and *Nebularia*, respectively. In its revised circumscription, *Parmeliella* is a mostly temperate genus including small-squamulose species, generally without chemical substances and apothecia without thalline margin but with an amyloid hymenium producing asci with an internal apical tube structure.

It is noteworthy that the likewise tropical *Parmeliella pannosa* (Sw.) Nyl., which is often confused with *P. mariana*, belongs in *Parmeliella sensu stricto*. *Parmeliella pannosa* has a narrow and tube-like amyloid apical structure typical of the genus, whereas *Lepidocollema* have a broader ring-like apical structure.

Pectenia P. M. Jørg., L. Lindblom, Wedin & S. Ekman *nom. et stat. nov*. (Fig. 2B)
for *Degelia* sect. *Amphiloma* (Fr.) P. M. Jørg. & P. James, Bibl. Lich. 38: 261 (1990).
MycoBank No.: MB

Generitype: *Pectenia plumbea* (Lightf.) P. M. Jørg., L. Lindblom, Wedin & S. Ekman.

Thallus blue-grey, placodioid, appearing thick and rigid, in orbicular patches up to 10 cm in diam, up to 250 µm thick. Upper cortex cellular, up to 40 µm thick. Photobiont layer 60–100 µm thick, with *Nostoc* cells 6–8 µm diam., in clusters. Medulla up to 150 µm thick, composed of parallel, branched, short-celled, horizontally aligned hyphae forming a compact plectenchyma, gradually merging into hypothallus. Hypothallus thick, felt-like, blue-black, often extending beyond the ascending marginal lobes.

Apothecia laminal, usually abundant, biatorine with brown disc and a paler rim. Proper exciple up to 100 µm wide, consisting of isodiametric cells. Subhymenial layers pale yellowish brown, up to 150 µm thick, composed of intricately interwoven hyphae. Hymenium 100–150 µm high, colourless except for brown pigment in uppermost part, I+ persistently blue. Paraphyses unbranched. Asci clavate to cylindrical, with an apical dark-amyloid plug. Ascospores 8 per ascus, colourless, ellipsoid with smooth wall and without perispore, non-septate.

Pycnidia infrequent, mostly marginal, protruding, black, up to 0.2 mm wide. Conidiophores short-celled, producing conidia terminally and laterally. Conidia bacilliform, 1–3 × 1 µm.

Chemistry: No lichen substances (Jørgensen & James 1990).

Etymology: From the Latin generic name of scallop, *Pecten,* due to the grooved scallop-like pattern often found on the upper surface of the species in this genus.

Notes: The name *Amphiloma* cannot be used at generic level, since it is occupied by two older homonyms (Jørgensen 1978). Consequently, we establish the new name *Pectenia* based on sect. *Amphiloma* and with the same type species, *P. plumbea*. *Pectenia* is mainly confined to Europe and adjacent Africa, mostly along the Atlantic coast. However, *P. plumbea* occurs also in a restricted region in North-East America (Blom & Lindblom 2009; Richardson *et al*. 2010).

Physma A.Massal. (Fig. 5D), previously treated in the Collemataceae, belongs in the Pannariaceae, as also shown by Wedin *et al*. (2009) and Otálora *et al*. (2010). In our phylogeny, *Physma* is the sister group to the *Parmeliella mariana* group, referred here to *Lepidocollema*. *Physma* is characterised by a leathery thallus with a dense upper pseudocortex (unlike the cellular cortex in *Lepidocollema*) and thick-walled ascospores with a markedly swollen epispore.

Protopannaria (Gyeln.) P. M. Jørg. & S. Ekman (Fig. 3B) is comprised of seven known crustose-squamulose species without secondary chemistry, apothecia with thalline margin, and amyloid hymenia with asci lacking internal amyloid structures (Jørgensen 2001a, 2001b, 2004, 2007; Øvstedal & Friday 2011). In our phylogeny, *P. pezizoides* is sister to *Santessoniella grisea* (Hue) Henssen (Fig. 7D). An undescribed species closely related to

Santessoniella crossophylla (Tuck.) P. M. Jørg. (Fig. 7C) is sister to *P. pezizoides* and *S. grisea*. Unlike *P. pezizoides*, the two species of '*Santessoniella*' have a hemiamyloid hymenium and an internal apical ring structure in the asci. These differences make it unlikely that they can be included in *Protopannaria*, despite strong branch support in our phylogeny. At the moment, we retain *Protopannaria* in its current circumscription and refrain from suggesting alternative classifications for the two species of '*Santessoniella*'. We note, however, that relationships and generic boundaries in this group are in need of further study.

Psoroma Ach. ex Michx (Fig. 5G) traditionally accommodated *Pannaria*-like species with a green algal photobiont and a thalline margin surrounding the apothecia. Jørgensen (2001a) restricted the circumscription of the genus to include close relatives of the type species *Psoroma hypnorum* (Vahl) Gray, i.e. small-squamulose, bryophilous species without lichen substances, and with an amyloid tube- or ring-like structure in the ascus apex. Branch support within Clade 2c in our phylogeny is poor and provides little guidance for revised generic delimitations. We provisionally retain *Psoroma* more or less as currently understood, with few amendments: '*Pannaria*' *dichroa* and '*P.*' *orphnina* (along with the two similar species '*P.*'*obscurior* and '*P.*' *xanthorioides*) are referred here to *Psoroma* despite their cyanobacterial photobiont, because our phylogeny provides support for their exclusion from *Pannaria*. Indeed, in accordance with their phylogenetic placement, the asci of these species have a wide amyloid ring structure, which can, however, be difficult to observe. '*Pannaria*' *orphnina* is the type species of the genus *Siphulina* (Hue) C. W. Dodge (Jørgensen 2005b), which accordingly becomes a taxonomic synonym of *Psoroma*. Furthermore, although *Psoroma tenue* does not form a monophyletic group with the rest of *Psoroma* in our phylogeny, there is no support for its exclusion. Chemically, however, *P. tenue* and its relatives deviate from the rest of *Psoroma* in producing porpypilic acid and related

substances. We refrain from transferring '*Santessoniella*' *arctophila*, sister to *P. tenue* with high support, to *Psoroma* or any other genus in the absence of a well resolved phylogeny. We have, however, chosen to include *Santessoniella polychidioides* (and its close relative *S. macrospora*) in *Psoroma*, because there is reasonable support (0.92 posterior probability) for a close relationship with *P. aphthosum* and because branch attachment frequencies calculated by Phyutility shows that the remaining posterior probability (0.08) is divided between two other positions nested inside our understanding of *Psoroma*. This choice makes *Santessoniella* a taxonomic synonym of *Psoroma*. With these amendments, *Psoroma* includes species with small-squamulose or rarely small-fruticose thalli with a green algal or cyanobacterial primary photobiont, and mostly lack of secondary chemistry (the presence of porphyrilic acid and related substances in *Psoroma tenue* and relatives being an exception, if included).

Our phylogenetic tree indicates that the widespread *P. hypnorum*, type species of the genus, is paraphyletic. Further investigations need to determine whether this observation is caused by incomplete lineage sorting or the occurrence of multiple species within *P. hypnorum* as currently delimited. *Psoroma hypnorum* specimen III deviates conspicuously from other specimens in having a cyanobacterial (*Nostoc*) photobiont instead of the standard primary green algal one (Holien & Jørgensen 2000). The cyanobacterial photobiont confers dramatic modifications to overall lichen morphology towards a growth form similar to taxa currently classified in *Santessoniella*. Our phylogeny indicates, however, that the fungal component of the cyanobacterial morph is closely related to at least some green algal representatives (here *P. hypnorum* specimen V; see Fig. 1). It should also be pointed out that the determination of the *P. fruticulosum* specimen used to generate the sequences was questioned by Passo *et al*. (2008).

Psoromaria Nyl. ex Hue may deserve recognition as a genus (see *Degeliella*). It originally contained two species, *P. subdescendens* Nyl. (=*Degeliella versicolor*) and *P. descendens* Nyl. (= *Psoromidium aleuroides*). The former was later selected as lectotype (Clements & Shear 1931: 319). Galloway & James (1985) treated both species in *Psoromidium* Stirt. (as *P. aleuroides* and *P. versicolor*), whereas Jørgensen (2004) referred *P. versicolor* to *Degeliella*, regarding it as the green counterpart of *D. rosulata*. In doing so, the older name *Psoromaria* was unfortunately overlooked. Although we note that *Psoromaria* may be available for *Degeliella versicolor* if treated as a separate genus, we refrain from nomenclatural changes at the moment, in anticipation of taxonomical clarifications in the group.

Psoromidium Stirt. was reinstated by Galloway & James (1985) for two species, the type species *P. wellingtonii* Stirt. (= *P. aleuroides* (Stirt.) D. J. Galloway) and *P. versicolor* (Hook. f. & Taylor) D. J. Galloway *nom illeg*. The latter was later transferred to the new genus *Degeliella* (see that genus). *Psoromidium aleuroides* is characterised by a thallus of close adpressed squamules with a green algal primary photobiont, resting on a distinct hypothallus, and distinct cephalodia with *Nostoc*, an amyloid hymenium, an ascus with an apical ring-structure, and lack of secondary chemistry (Galloway & James 1985). Apart from the evanescent apothecial thalline margin in species of *Psorophorus* (Elvebakk *et al*. 2010), morphology suggests a close relationship between the two genera. If proven synonymous, *Psoromidium* is the older name. We provisionally retain *Psoromidium*, although we note that further studies are needed.

Psorophorus Elvebakk & Hong (Fig. 5F) was recently described by Elvebakk *et al*. (2010) for the type species *P. pholidotus* (Mont.) Elvebakk and *P. fuegiensis* (Zahlbr.) Elvebakk & Hong. Both species were included in our phylogeny and together form a well supported

monophyletic group sister to *Austroparmeliella lacerata*. The relationship with *Psoromidium* needs further study (see that genus).

Ramalodium Nyl. (Fig. 4A) currently comprises six species, *R. succulentum* Nyl. being the type (Henssen 1965, 1979, 1999). We included only the type species in our phylogeny (as did Wedin *et al*. 2009). *Ramalodium succulentum* is recovered as sister to *Staurolemma*. *Ramalodium* and *Staurolemma* have been considered closely related on morphological grounds, the main difference between the genera being the lecideine apothecia in *Ramalodium* and zeorine apothecia in *Staurolemma* (Henssen 1999).

Santessoniella Henssen (Fig. 6B), the type species of which is *S. polychidioides* (Zahlbr.) Henssen (Fig. 6B), was originally established by Henssen (1997) for a set of six small, often subfruticose and sometimes gelatinous species with *Parmeliella*-like apothecia (Henssen 1997). The genus continued to be used in this sense, and another seven species have later been described or transferred to that genus (Jørgensen 1998, 1999, 2005a; Henssen 2000; Henssen & Kantvilas 2000; Spribille *et al*. 2007; Jørgensen & Palice 2010).

Our phylogeny includes five species of *Santessoniella*, the type species *S. polychidioides*, *S. arctophila*, *S. saximontana*, an undescribed species close to *S. crossophylla*, and S. *grisea*. These species are dispersed across much of the tree and constitutes the most extreme example of genus-level non-monophyly in our investigation. The type species *Santessoniella polychidioides* is nested inside *Psoroma* with moderate support. Morphologically, it may be considered a cyanobacterial expression of a *Psoroma*, not unlike the cyanobacterial morph of *P. hypnorum* (Holien & Jørgensen 2000; *P. hypnorum* III in our tree). It is noteworthy, however, that the asci of *S. polychidioides* and relatives are more narrowly cylindrical than in *Psoroma sensu stricto*, with a tube-like amyloid internal structure

as opposed to the wider ring-like structure in *Psoroma sensu stricto*. In addition, the hymenial reaction is more pronouncedly hemiamyloid in *S. polychidioides* and relatives, rapidly changing from blue-green to red-brown, whereas in *Psoroma sensu stricto* the reaction is blackish blue, turning slowly to sordid blue. *S. saximontana* is nested inside *Leciophysma* with high support and seems to share morphological characteristics of that genus (Henssen 1965). *Santessoniella grisea* and the undescribed relative of *S. crossophylla* are closely related with *Protopannaria*, from which they differ markedly with respect to morphology. Finally, *S. arctophila* seems to be closely related to *Psoroma tenue*. Their relationships remain unclear and we refrain here from assigning them to a genus.

Siphulastrum Müll. Arg. (Fig. 2F) is a genus of four species, one of which is the type species *S. triste* Müll. Arg. (Jørgensen 2003). The genus is characterised by a heteromerous thallus with a *Scytonema* photobiont, a hemiamyloid hymenial reaction, lack of apical structures in the asci, presence of argopsin in the thallus, and a dense upper cortex of incrassate cells with small cell lumina. Unfortunately, material of the type species itself was not available for our study, although the included species, *S. squamosum*, conforms to the generic characteristics and is likely to be closely related to the type species. In our phylogenetic tree, *Siphulastrum* is the sister group to *Leioderma* and *Degeliella rosulata*.

Staurolemma Körb. (Fig. 4B) includes eight known species (Jørgensen 2010) and is typified by *S. dalmaticum* Körb., a synonym of *S. omphalarioides* (Anzi) P. M. Jørg. & Henssen. We included two species in our phylogeny, which form a monophyletic group with high support. Furthermore, *Staurolemma* is the sister group to *Ramalodium* in our phylogeny as well as that of Wedin *et al*. (2009). This corroborates the view that the two genera are closely related on morphological grounds, mainly differing in apothecial anatomy (Henssen 1999).

Note that '*Staurolemma* sp. nov.' included in the phylogeny of Wedin *et al*. (2009) has been described as *S. oculatum* P. M. Jørg. & Aptroot (Jørgensen 2010).

Steineropsis T. Sprib. & Muggia was described for the single species *S. alaskana* T. Sprib. & Muggia by Spribille *et al*. (2010). This species superficially resembles a *Placopsis* and the thallus is characterised by a paraplectenchymatous upper cortex, which extends into the medulla. Apothecia and pycnidia have not been described. *S. alaskana* was sister to *Protopannaria* in the phylogeny of Spribille & Muggia (2013).

Xanthopsoroma Elvebakk & Hong (Fig. 5H) was established to accommodate the type species *X. contextum* (Stirt.) Elvebakk and *X. soccatum* (R. Br. ex Crombie) Elvebakk, two Southern Hemispheric species previously treated in *Psoroma* and containing usnic acid and a series of terpenoids (Elvebakk *et al*. 2010). Support for its monophyly in our phylogeny is poor. Surrounding branches have high support, but we cannot exclude the possibility that *Xanthopsoroma* is paraphyletic. However, at least one, possibly both members of the genus are likely to be sister to Clade 2a-c (Fig. 1).

Provisional key to genera

1. Thallus gelatinous, mostly without lichen acids (PD-) … 2

- Thallus not gelatinous, often with lichen acids (PD+) … 11

2. Thallus subfruticose to fruticolose, sometimes nearly granular … 3

- Thallus squamulose to foliose … 5

3. Thallus applanate, finely and dichotomously dissected; photobiont *Scytonema*; medullary hyphae parallel to cortex; tropical … *Leptogidium*

- Thallus erect, consisting of coarser and often irregular branches; photobiont *Nostoc*; medullary hyphae at an angle to the cortex, usually in a reticulate pattern; temperate … 4

4. Lobes up to 0.3 mm wide, sometimes nearly granular; hyphal walls distinctly gelatinized … *Leciophysma*

- Lobes up to 1 mm wide, more or less squamulose; hyphal walls not or weakly gelatinized … *Psoroma pro parte* (‘*Santessoniella*’ *sensu stricto*)

5. Apothecia without thalline margin; thallus mostly squamulose or nearly subfruticose; Southern Hemisphere … 6

- Apothecia with thalline margin; thallus with wider, flattened lobes, subfoliose to foliose; tropical … 7

6. Thallus membranaceous; excipulum annular; asci with internal apical amyloid ring or tube … *Homothecium*

- Thallus squamulose (to subfruticose); excipulum cupular; asci without internal apical amyloid structures … *Ramalodium*

7. Thallus with fan-shaped lobes, tawny, with pannarin (PD+); asci without internal apical amyloid structures … *Pannaria lurida* group

- Thallus with narrow, elongated lobes, bluish grey, without pannarin (PD-); asci with internal apical amyloid ring-structures … 8

8. Thallus homoiomerous, containing terpenoids; ascospores globose, faintly brownish…… *Kroswia*

- Thallus heteromereous, without secondary substances; ascospores ellipsoid, colourless … 9

9. Thallus resting on a distinct mat of protruding blackish rhizohyphae; cortex cellular, one-layered; Brazil … *Lepidocollema carassense*

- Thallus without protruding rhizohyphae; cortex multi-layered; paleotropical … 10

10. Thallus with narrow, elongated lobes; cortex of 1–3 cell layers; apothecia stipitate without supportive tissue; Sri Lanka … *Leightoniella zeylanica*

- Thallus with wider lobes; cortex of densely agglutinated hyphae; apothecia sessile with supportive tissue; widespread in the tropics … *Physma*

11. Thallus with green-algal photobiont … 12

- Thallus with cyanobacterial photobiont … 19

12. Asci without internal amyloid apical structures ... 13

- Asci with internal amyloid apical structures ... 14

13. Thallus squamulose-foliose, with pannarin and related substances (PD+); apothecia with thalline margin… *Pannaria*

- Thallus of closely adpressed squamules, without secondary substances; apothecia biatorine, without thalline margin ... *Degeliella versicolor*

14. Squamules with a yellow tinge, with usnic acid … *Xanthopsoroma*

- Squamules without a yellow tinge, without usnic acid … 15

15. Apothecia often proliferating, without thalline margin; thallus with cottony prothallus … *Psoromidium*

- Apothecia single, with distinct thalline margin; thallus without cottony prothallus … 16

16. Thallus with pannarin (PD+); asci with distinct apical amyloid cap … *Joergensenia cephalodina*

- Thallus without pannarin (PD-); asci with amyloid apical ring-structures … 17

17. Apothecia flat, often with convex, dark-brown disc … *Fuscopannaria viridescens*

- Apothecia urceolate with concave, light or orange-brown disc … 18

18. Squamules appressed, resting on a distinct blackish prothallus; corticolous … *Psorophorus*

- Squamules loosely scattered over the substrate, without prothallus; usually bryophilous or terricolous … *Psoroma*

19. Thallus of closely appressed, chestnut brown squamules with cream-coloured soralia; hypothallus blue-black; photobiont *Nostoc*; nearly always sterile; Atlantic-Mediterranean … *Nevesia sampaiana*

- Thallus with different combination of characters ... 20

20. Thallus a small, placodioid, Placopsis-like rosette with opuntioid lobules and a thick, paraplectenchymatous upper cortex; sterile ... *Steineropsis alaskana*

- Thallus with different combination of characters ... 21

21. Apothecia with secondary thalline margin … 22

- Apothecia without secondary thalline margin, or rarely with thalline corona … 25

22. Thallus on distinct blackish hypothallus, without lichen substances or pigments; tropical … *Lepidocollema*

- Thallus not on distinct hypothallus, often with lichen substances or pigments … 23

23. Thallus squamulose-foliose, usually with pannarin (PD+); asci without internal, apical amyloid structures … *Pannaria*

- Thallus small-squamulose, usually without pannarin (PD-), rarely with pannarin (but then also with argopsin); asci with internal amyloid ring-structures … 24

24. Apothecia with distinct thalline margin, disc orange-brown, hymenium amyloid … *Protopannaria*

- Apothecia with variably developed thalline margin, disc brown to blackish; hymenium hemiamyloid … *Fuscopannaria*

25. Thallus foliose, not closely appressed to substrate, upper surface usually with hairs … 26

- Thallus sqamulose or placodioid, often closely appressed to substrate, upper surface without hairs … 27

26. Thallus always hairy, often with stiff prominent hairs; apothecia usually marginal and stalked, if otherwise always PD+ orange (eriodermin) … *Erioderma*

- Thallus arachnoid-tomentose or glabrous, with laminal, sessile apothecia, PD- … *Leioderma*

27. Thallus placodioid, often forming large circular blue-grey thalli with well-developed bluish black rhizohyphae … 28

- Thallus not placodioid, without or with brownish rhizohyphae … 31

28. Hymenium non-amyloid; asci without internal apical amyloid structures; photobiont *Scytonema*… *Degeliella rosulata*

- Hymenium amyloid; asci with internal apical amyloid structures; photobiont *Scytonema* or *Nostoc* … 29

29. Thallus thin and *Coccocarpia*-like, with a *Scytonema* photobiont; upper cortex prosoplectenchymatous, consisting of a few cell layers of periclinally arranged hyphae; Southern Hemisphere … *Degelia* sect. *Degelia*

- Thallus thick and rigid; upper cortex paraplectenchymatous, consisting of several layers of anticlinally arranged hyphae ... 30

30. - Photobiont *Nostoc*; thallus losely attached to substrate, with upper surface having prominent longitudinal ridges; Northern Hemisphere … *Pectenia*

- Photobiont *Scytonema*, thallus appressed to substrate, with smooth upper surface; Subantarctic ... *Degelia* sect. *Frigidae*

31. Apothecia surrounded by a thin weft of hyphae; asci narrowly elongate, thin-walled, without internal apical structures … *Austrella*

- Apothecia not surrounded by a weft of hyphae; asci wider, clavate to cylindrical, thick-walled, with internal apical amyloid structures … 32

32. Apothecia with thick proper exciple, containing elements of the formative supporting tissue and photobiont cells penetrating into the subhymenium … 33

- Apothecia with thin proper exciple, without supporting tissue or photobiont cells in the subhymenium … 34

33. Lower surface with small, curled brownish hairs; hymenium hemiamyloid; Southern Hemisphere… *Fuscoderma*

- Lower surface without brownish hairs; hymenium amyloid; Andean Mountains … *Nebularia*

34. Thallus thick and often shiny, containing argopsin (PD+); cortical cells thick-walled; hymenium hemiamyloid; mostly terricolous ... *Siphulastrum*

- Thallus thin and usually dull, without argopsin (PD-); cortical cells thin-walled; hymenium amyloid; mostly corticolous … 35

35. Thallus often forming both upper and lower cortex; subhymenium flat, colourless … *Austroparmeliella*

- Thallus only with upper cortex; subhymenium often lentil-shaped, brownish … *Parmeliella*

New species-level combinations

In this section, we list species-level combinations necessitated by the generic classification proposed above.

Austroparmeliella chilensis (Hue) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Placynthium chilense Hue, *Bull. Soc. Linn. Normandie ser. 5,* **9**: 158–159 (1906); type: Chile. Cordillera de Ranco, *Lechler* 3016 (PC—lectotype! *fide* Henssen 1997: 83).

Austroparmeliella elongata (Henssen) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Santessoniella elongata Henssen, Symb. Bot. Ups. **32**: 83–84 (1997); type: Argentina. Rio Negro, Parque Nacional Nahuel Huapi, Puerto Blest, 1973, *Vobis & Henssen* 24606a (H—holotype!).

Austroparmeliella lacerata (P. M. Jørg.) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Parmeliella lacerata P. M. Jørg., *Lichenologist* **30:** 537 (1998); type: Republic of South Africa. Western Cape, Riviersonderend, Oubos Forest, 1996, *Nordin* 4542 (UPS—holotype!).

Austroparmeliella rakiurae (P. M. Jørg.& D. J. Galloway) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Parmeliella rakiurae P. M.Jørg. & D.J.Galloway, *Bibl*. *Lich*. **88:** 244 (2004); type: New Zealand. Stewart Island, Port Pegasus, track from Disappointment Cove to Broad Bay, coastal forest on *Olearia* bark, 29.vii.2001, *Galloway* 0845 (BG—holotype!).

Austroparmeliella rosettiformis (Henssen) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Santessoniella rosettiformis Henssen, *Lichenologist* **32:** 18 (2000); type: Chile. Prov. Arauco, Parque Nacional Contulma, 1973, *Vobis & Henssen* 24281 (H—holotype!).

Leciophysma saximontana (T. Sprib., P. M. Jørg. & M. Schulz) P. M. Jørg., Wedin & S. Ekman *comb*. *nov*.

MycoBank No.: MB

Santessoniella saximontana T. Sprib., P. M. Jørg. & M. Schulz, *Bibl. Lich*. **98:** 288 (2007); type: Canada. British Columbia, Rocky Mts., Albert River drainage, 2006, *Spribille* 21173 & *Houde* (CANL—holotype!)

Lepidocollema adpressum (P. M. Jørg.) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Parmellia adpressa P. M. Jørg., *Journ. Japanese Bot*. **76:** 289 (2001); type: Japan. Shinano prov., Mt. Kinpu, alt. 2100-2450 m, *Jinzenji* 176 (TNS—holotype!).

Lepidocollema allochroum (Makhija & Adaw.) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Parmeliella allochroa Makhija & Adawad, *Mycotaxon* **71:** 327 (1999); type: India. Nicobar Islands, Car Nicobar, Kimus, on coconut palm, 29.xii.1986, *Patwardhan & Sethy* 86.787 (AMH—holotype!).

Lepidocollema borbonicum (P. M. Jørg. & Schumm) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Parmeliella borbonica P. M. Jørg. & Schumm, *Lichenologist* **42:** 697 (2010); type: La Réunion. Takamaka, low mountain forest near the electrostation, alt. 790 m, 10.ix.2009, *Frahm & Schumm* (BG—holotype!).

Lepidocollema brisbanense (C. Knight) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Pannaria brisbanensis C. Knight in J. Shirley, *Proc. Royal Soc. Queensland* **6:** 194 (1890); type: Australia. Queensland, Brisbane River, *Shirley* 113 (WELT—lectotype! *fide* Jørgensen & Galloway 1992).

Lepidocollema cineratum (Zahlbr.) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Pannaria cinerata Zahlbr. in H. Magn. & Zahlbr., *Ark. Bot.* **31A(1):** 72 (1943); type: U.S.A. Hawaii, Kauai, Kauhao, 1000 m, 8.ii.1910, *Faurie* 274 (W—holotype!).

Lepidocollema endoluteum (P. M. Jørg.) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Parmeliella endolutea P. M. Jørg., *Lichenologist* **39:** 239 (2007); type: Philippines. Prov. Rizal, Mt. Irid, *Herre* (LAM—holotype!).

Lepidocollema endomiltum (Vain.) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Pannaria endomilta Vain., *Ann. Acad. Sci. Fenn.* ser.A 15, **6:** 15 (1921); type: Philippines. Mindanao, Davao, Mt. Apo, 6000 ft., 21.iv.1904, *Copeland* 1090 *p.p.* (TUR-V 12168—holotype!).

Lepiodocollema exornatum (Zahlbr.) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Pannaria cinerata var. *exornata* Zahlbr. in H. Magn. & Zahlbr., *Ark. Bot.* **31A(1):** 72 (1943); type: U.S.A. Hawaii, Maui, Hana, ix.1909, *Faurie* 559 (W—lectotype! *fide* Jørgensen 2003).

Lepidocollema flavidum (P. M. Jørg.) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Parmeliella flavida P. M. Jørg., *Bryologist* **106:** 123 (2003); type: Philippines. Luzon, Basilan, Basilan Lumber Company logging area, 25 km N of Upper Canas, vi.1964, *Hale & Banaag* (US—holotype!).

Lepidocollema fuscatum (P. M. Jørg.) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Parmeliella fuscata P. M. Jørg., *Bryologist* **106:** 123 (2003); type: India. Maharasta, Ambenali, on road to Pratapgad, felled tree at bridge, 2.xi.1973, *Hale* 40045 (US—holotype!).

Lepidocollema granuliferum (P. M. Jørg.) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Parmeliella granulifera P. M. Jørg., *Bibl*. *Lich*. **78:** 129 (2001); type: Australia. Northern Territory, Channel Island, prawn farm, landward edge of mangroves, 1991, *Benfield* (BRI—holotype!).

Lepidocollema imbricatulum (Müll. Arg.) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Pannaria imbricatula Müll.Arg., *Flora* **64:** 507 (1881); type: Brazil. São Paolo, prope Apiahy, *Puiggari* 148 *p.p*. (G—holotype!).

Lepidocollema leiostromum (Nyl.) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Pannaria leiostroma Nyl. in Leight., *Trans*. *Linn*. *Soc*. *London* **27:** 165 (1869); type: Sri Lanka, *Thwaites* (BM—holotype!).

Lepidocollema macrosporum (Makhija & Adawad.) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Parmeliella macrospora Makhija & Adawad., *Mycotaxon* **71:** 332 (1999); type: India. Nicobar Island, Car Nicobar, Kimus, 1986, *Sethy & Nagarkar* 86.778 (AMH—holotype!).

Lepidocollema marianum (Fr.) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Parmelia mariana Fr., *Syst*. *Orb*. *Veg*. **I:** 284 (1825); type: Mariana Islands, *Gaudichaud* (UPS—holotype!).

Lepidocollema montanum (P. M. Jørg. & Sipman) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Parmeliella montana P. M. Jørg. & Sipman, *J*. *Hattori Bot*. *Lab*. **100:** 711 (2006); type: Papua New Guinea. Morobe Distr., Mt. Kaindi, Wau, 1973, *Kashiwadani* 10541 (TNS—holotype!).

Lepidocollema nitidum (P. M. Jørg. & Sipman) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Parmeliella nitida P. M. Jørg. & Sipman, *J*. *Hattori Bot*. *Lab*. **100:** 712 (2006); type: Papua New Guinea. Simbu Prov., Mt. Wilhelm, Pindaunde valley, near hut on S-shore of Lake Piunde, W slope of valley, *c*. 3700 m, 6.iix.1992, *Sipman* 35688 (B—holotype!).

Lepidocollema pannarioides (P. M. Jørg. & Sipman) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Parmeliella pannaroides P. M. Jørg. & Sipman, *J. Hattori Bot. Lab*. **100:** 713 (2006); type: Papua New Guinea. Western Highland Distr., Mt. Wilhelm, en route from Kombugomanubo to the Pindaunde Lakes, 1974, *Kashiwadani* 11064 (TNS—holotype!).

Lepidocollema papillatum (P. M. Jørg.) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Parmeliella papillata P. M. Jørg., *Bibl. Lich.* **78:** 133 (2001); type: Australia. Queensland, Cardwell Range, 45 km NW of Cardwell, 1986, *Elix* 20169 *& Streimann* (CANB—holotype!).

Lepidocollema polyphyllinum (P. M. Jørg.) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Parmeliella polyphyllina P. M. Jørg., *Bibl. Lich.* **78:** 134 (2001); type: Australia. Queensland, Hugh Nelson Range, along Plath Road, 15 km S of Atherton, alt. 1080 m, 25.vi.1984, *Elix* 16363 *& Streimann* (CANB—holotype!).

Lepidocollema stylophorum (Vain.) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Pannaria stylophora Vain., *Add. Lichenogr. Antill.*: 102 (1915); type: Guadeloupe. Sofaga, ad corticem Sapii aucupari, *Duss* 1387 (TUR-V 12107—holotype!).

Lepidocollema wainioi (Zahlbr.) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Pannaria wainioi Zahlbr., *Cat*. *Lich*. *Univ*. **3:** 261 (1924); type: Philippines. Mindanao, Butuan, alt. 15 m, 1911, *Weber* 1387 (TUR-V 12178—lectotype! *fide* Jørgensen 2003).

Lepidocollema zeylanica (P. M. Jørg.) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Parmeliella zeylanica P. M. Jørg., *Lichenologist* **41:** 257 (2009); type: Sri Lanka. Nuwara Elyia, near the Golf Club, 1964, *Degelius* As-438 (UPS—holotype!).

Nebularia incrassata (P. M. Jørg.) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Parmeliella incrassata P. M. Jørg., *Lichenologist* **32:** 141 (2000); type: Ecuador. Pichincha, eastern slopes of Cerro Iliniza, alt. 4200 m, epiphyte on *Polylepis*, 7.iii.1972, *Arvidsson & Nilsson* (GB—holotype!).

Nebularia psoromoides (P. M. Jørg. & Palice) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Parmeliella psoromoides P. M. Jørg. & Palice, *Nordic J*. *Bot*. **28:** 625 (2010); type: Ecuador. Carchi, Volcan Chiles, paramo ca 1.5 km southwest of the top, 4050 m a.s.l., 13.vii.1999, *Palice* 11977 (PRA—holotype!).

Nevesia sampaiana (Tav.) P. M. Jørg., L. Lindblom, Wedin & S. Ekman *comb*. *nov*.

MycoBank No.: MB

Pannaria sampaiana Tav., *Port*. *Acta Biol*. ser. B **3:** 76–77 (1950); type: Portugal. Minho, Serra do Gerês, between S. Bento da Porta Alberta and Freitas, 1948, *Tavares* 2829 (LISU—holotype!).

Pectenia atlantica (Degel.) P. M. Jørg., L. Lindblom, Wedin & S. Ekman *comb*. *nov*.

MycoBank No.: MB

Parmeliella atlantica Degel., *Acta Phytogeogr*. *Suec*. **7:** 131 (1935); type: Ireland. Killarney, near Muckross lake, 1933, *Degelius* (UPS—holotype!).

Pectenia cyanoloma (Schaer.) P. M. Jørg., L. Lindblom, Wedin & S. Ekman *comb*. *nov*.

MycoBank No.: MB

Parmelia plumbea var *cyanoloma* Schaer., *Enum*. *Criticae Lich*. *Eur*.: 36 (1850); type: France. Normandie, in sylva Briquebec, *Delise* (G—lectotype! *fide* Jørgensen 1978)

Pectenia ligulata (P. M. Jørg. & P. James) P. M. Jørg., L. Lindblom, Wedin & S. Ekman *comb*. *nov*.

MycoBank No.: MB

Degelia ligulata P. M. Jørg. & P. James, *Bibl*. *Lich*. **38:** 266 (1990); type: Portugal. Azores, Faial, Santa Maria, Anjos, on mossy earth bank, 1976, *James* (BM—holotype!).

Pectenia plumbea (Lightf.) P. M. Jørg., L. Lindblom, Wedin & S. Ekman *comb*. *nov*.

MycoBank No.: MB

Lichen plumbes Lightf., *Fl*. *Scot*. **2:** 826 (1777); type: Great Britain (OXF-DILL 179: 73a—lectotype! *fide* Jørgensen 1978).

Psoroma dichroum (Hook. f. & Taylor) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Lecanora dichroa Hook.f. & Taylor, *J. Bot. London* **3:** 643 (1844); type: Kerguelen. Christmas harbour, *Hooker* 1844 (FH—lectotype! *fide* Dodge 1948.)

Psoroma macrosporum (P. M. Jørg. & Palice) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Santessoniella macrospora P. M. Jørg. & Palice, *Nord. J. Bot.* **28:** 626 (2010); type: Ecuador. Carchi: surroundings of Laguna Verde, 1.5–1.8 km SSE of Volcan Chiles, 4000 m a.s.l., 12.vii.1999, *Palice* 2750 (PRA—holotype!).

Psoroma obscurior (Nyl.) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Pannaria obscurior Nyl. in Cromb., *J. Bot. London* **13:** 334 (1875); type: Kerguelen. Observatory Bay, xii.1874, *Eaton* (BM—holotype!).

Psoroma orphninum (Hue) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Siphula orphnina Hue, *2me Exped. Antarct. FranV., Lich.*: 19 (1915); type: South Shetland. Livingston Isl., South Bay, Johnson's Peak, 300–350 m, 8.ii.1998, *Søchting* 7833 (BG—neotype! *fide* Jørgensen 2005b).

Psoroma polychidioides (Zahlbr.) P. M. Jørg. *comb. nov.*

MycoBank No.: MB

Lemmopsis polychidioides Zahlbr. in Skottsb.: *Nat. Hist. of Juan Fernandez Easter Isl.* **2:** 333 (1924); type: Chile. Juan Fernandez, Mastierra, Cordon Chifladores, 17.iv.1917, *Skottsberg & Skottsberg* 408 (UPS—holotype!).

Psoroma xanthorioides (P. M. Jørg.) P. M. Jørg. *comb*. *nov*.

MycoBank No.: MB

Pannaria xanthorioides P. M. Jørg., *Bibl*. *Lich*. **88:** 238 (2004); type: Heard Island. Near the summit of Scarlet Hill, 6.i.2001, *Gremmen* H-0663 (CANB—holotype!).

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FIGURE LEGENDS

FIG. 1. Majority-rule consensus tree with all compatible groups and average branch lengths resulting from Bayesian MCMC with PhyloBayes under an F81+Γ+CAT model on concatenated data from *ITS*, *mrSSU*, and *RPB1*. Bayesian posterior probabilities are indicated. *Vahliella leucophaea* in the Vahliellaceae is the outgroup. Names generally follow Jørgensen (2003), although our interpretation of generic affinities (resulting from this phylogeny, other published phylogenies cited in the text, as well as morphological data) is indicated with white text against a black background. Four main clades (1, 2a, 2b, and 2c) are indicated in colour. Roman numbers are used to distinguish specimens of the same taxon. Coloured dots after taxon names indicate the type of primary photobiont (blue = cyanobacterial, green = green algal photobiont).

FIG. 2. Representatives of Clade 1. A, *Degelia gayana*; B, *Pectenia plumbea*; C, *Degeliella rosulata*; D, *Parmeliella triptophylla*; E, *Joergensenia cephalodina*; F, *Siphulastrum squamosum*; G, *Leioderma pycnophorum*; H, *Erioderma leylandii*. Photos: Jan Berge.

FIG. 3. Representatives of Clade 2a. A, *Nevesia sampaiana*; B, *Protopannaria pezizoides*; C, *Leciophysma finmarkicum*; D, *Fuscopannaria leucosticta*. Photos: Jan Berge.

FIG. 4. Representatives of Clade 2b. A, *Ramalodium succulentum*; B, *Staurolemma omphalarioides*; C, *Pannaria rubiginosa*. Photos: Jan Berge.

FIG. 5. Representatives of Clade 2c and *Xanthopsoroma*. A, *Nebularia incrassata*; B, *Fuscoderma applanatum*; C, *Austroparmeliella lacerata*; D, *Austrella arachnoidea*; E, *Lepidocollema marianum*; F, *Physma byrsaeum*; G, *Psorophorus pholidotus*; H, *Psoroma hypnorum*; I, *Xanthopsoroma contextum*. Photos: Jan Berge.

FIG. 6. Type species of two abandoned genera. A, *Moelleropsis nebulosa*, referred here to *Fuscopannaria*; B, *Santessoniella polychidioides*, referred here to *Psoroma*. Photos: Jan Berge.

FIG. 7. Five members of the Pannariaceae with uncertain generic affiliation. A, *Pannaria isabellina*; B, *Pannaria hispidula*; C, *Santessoniella crossophylla*; D, *Santessoniella grisea*; E, *Degeliella versicolor*. Photos: Jan Berge.