

1 **Molecular systematics and character evolution in the lichen family Ramalinaceae (Lecanorales,**  
2 **Ascomycota)**

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4 Sonja Kistenich<sup>1\*</sup>, Einar Timdal<sup>1</sup>, Mika Bendiksby<sup>1,2</sup> & Stefan Ekman<sup>3</sup>

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6 <sup>1</sup> Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, 0318 Oslo, Norway

7 <sup>2</sup> NTNU University Museum, Norwegian University of Science and Technology, Elvegata 17, 7012

8 Trondheim, Norway

9 <sup>3</sup> Museum of Evolution, Uppsala University, Norbyvägen 16, 75236 Uppsala, Sweden

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11 \* Corresponding author: s.d.kistenich@nhm.uio.no

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18           **Abstract** The Ramalinaceae is the fourth largest family of lichenized ascomycetes with 42 genera  
19 and 913 species exhibiting considerable morphological variation. Historically, generic boundaries in the  
20 Ramalinaceae were primarily based on morphological characters. However, molecular systematic  
21 investigations of subgroups revealed that current taxonomy is at odds with evolutionary relationships.  
22 Tropical members of the family remain particularly understudied, including the large genus *Phyllopsora*.  
23 We have generated and collected multilocus sequence data (mtSSU, nrITS, nrLSU, RPB1, RPB2) for 149  
24 species associated with the Ramalinaceae and present the first comprehensive molecular phylogeny of the  
25 family. We used ancestral state reconstructions on our molecular family phylogeny to trace the evolution  
26 of character states. Our results indicate that the Ramalinaceae have arisen from an ancestor with long,  
27 multiseptate ascospores living in humid temperate forests, and that the phylloporoid growth form has  
28 evolved multiple times within the family. Based on our results using integrative taxonomy, we discuss  
29 sister-relations and taxon-delimitation within five well-supported clades: The *Bacidia*-, *Biatora*-,  
30 *Ramalina*-, *Rolfidium*-, and *Toninia*-groups. We reduce six genera into synonymy and make 49 new  
31 nomenclatural combinations. The genera *Bacidia*, *Phyllopsora*, *Physcidia* and *Toninia* are polyphyletic  
32 and herein split into segregates. We describe the two genera *Bellicidia* and *Parallopsora* and resurrect the  
33 genera *Bibbya*, *Kiliasia*, *Thalloidima* and *Sporacestra*. According to our new circumscription, the family  
34 Ramalinaceae now comprises 38 genera.

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36           **Keywords** Ancestral state reconstruction, integrative taxonomy, multilocus phylogeny,  
37 *Phyllopsora*, *Toninia*, tropical lichens

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39           **Supplementary Material** The Electronic Supplement (Tables S1–S2; Figs. S1–S2) is available in  
40 the Supplementary Data section of the online version of this article (xx).

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## INTRODUCTION

The Ramalinaceae C. Agardh is the fourth largest family of lichen-forming ascomycetes, with 42 genera and 913 species (Lücking & al. 2017a, b). This family contains members with a chlorococcoid photobiont, mostly biatorine or lecideine apothecia (when present) and hyaline and often transversely septate ascospores. Historically, generic boundaries were primarily based on growth form, ascospore septation and even ecological preferences. Growth form varies considerably among species. The majority of species form crustose or squamulose thalli, but fruticose or foliose species occur in a couple of genera. Members of the family inhabit a wide spectrum of habitats, including lichenicolous life forms, but corticolous and saxicolous species are the most numerous. Being globally distributed, the Ramalinaceae span all climatic zones from arctic to temperate and tropical, and occur in humid as well as dry habitats.

The Ramalinaceae, as currently circumscribed (sensu Lücking & al. 2017a, b), has been variously delimited in the past. Originally, it was described by Agardh in 1821 as ‘Ramalineae’ and included the eight genera *Sphaerophoron* (now *Sphaerophorus*, Sphaerophoraceae), *Roccella* (Roccellaceae), *Evernia* (Parmeliaceae), *Dufourea* (Teloschistaceae), *Alectoria* (Parmeliaceae), *Ramalina* (Ramalinaceae), *Cornicularia* (Parmeliaceae) and *Usnea* (Parmeliaceae; Agardh 1821). More than 100 years later, Watson (1929) excluded all other genera besides *Ramalina* and was the first to use the correct family name, Ramalinaceae. Zahlbruckner (1921–1940) assigned some foliose and fruticose genera to this family, while crustose species now included here were placed by him in the family Lecideaceae Chevall. He divided the genus *Ramalina* into three sections: *Ecorticatae*, *Desmaziera* and *Euramalina* (Zahlbruckner 1921–1940). Keuck (1979) was the first to investigate morphological and anatomical features of the family’s – at that point – five genera: *Cenozosia*, *Niebla*, *Ramalina*, *Ramalinopsis* and *Trichoramalina*. Crustose genera were at the time still included in other families, for example Bacidiaceae Walt. Watson, Biatoraceae A. Massal. ex Stizenb., Lecaniaceae Walt. Watson, Lecideaceae, and Phyllopsoraceae Zahlbr. In his extensive work, Hafellner (1984) reclassified the large families Lecanoraceae and Lecideaceae and erected the following additional families for some of the genera now placed in Ramalinaceae:

Catillariaceae Hafellner, Catinariaceae Hale ex Hafellner, Crocyniaceae M. Choisy ex Hafellner, Megalariaceae Hafellner, Mycobilimbiaceae Hafellner, and Schadoniaceae Hafellner. Later, most of those families were reduced into synonymy with Bacidiaceae (see Ekman 2001 for a thorough historical overview). Ekman (2001) investigated taxa belonging to both Bacidiaceae and Ramalinaceae in a broad molecular phylogeny and pointed out the striking morphological similarities in the ascus structure between the two families. The inclusion of the Bacidiaceae, Megalariaceae (Ekman 2001), and later Crocyniaceae (Ekman & al. 2008) resulted in 42 component genera (Lücking & al. 2017a, b). Even so, the synonymy of Bacidiaceae with Ramalinaceae does not seem to have been broadly accepted, as the Bacidiaceae as a separate family is still being used in some modern literature (e.g., Sérusiaux & al. 2012).

The first molecular studies of the Ramalinaceae that included more than five genera (e.g., Ekman 2001; Reese Næsborg & al. 2007; Schmuil & al. 2011; Miadlikowska & al. 2014) rendered the family circumscription non-monophyletic as several genera and species were nested in other lichen families. A few Ramalinaceae genera have undergone further molecular phylogenetic investigations, for example *Bacidia* De Not. (Ekman 2001), *Biatora* Fr. (Printzen 2014), and *Lecania* A. Massal. (Reese Næsborg & al. 2007). None of these, however, included a family-wide taxonomic sampling, which left most generic boundaries largely unexamined, while at the same time rendering these genera polyphyletic. The recent compilation by Lücking & al. (2017a, b) reported that only 55% of the 42 Ramalinaceae genera are represented by DNA sequence data in GenBank, and less than half of those genera have ten or more sequence records. Despite recent molecular efforts to delimit the family within Lecanorales (Miadlikowska & al. 2014), comprehensive phylogenetic investigations of the family with an exhaustive genus-level sampling have so far not been conducted. Genera lacking molecular sequences to verify their placement in the Ramalinaceae include the enigmatic *Heppsora* D.D. Awasthi & Kr.P. Singh, *Physcidia* Tuck., *Pseudohepatica* P.M. Jørg., and *Tasmidella* Kantvilas, Hafellner & Elix, among others (Lücking & al. 2017a, b: Table S1).

While many morphological studies and monographs have been published on temperate species of the Ramalinaceae in North America and Europe (Howe 1913a, 1913b; Mayrhofer 1988; Timdal 1992; Printzen 1995; Ekman 1996a; Printzen and Tønberg 1999), tropical members of the family remain understudied. A set of genera occurring almost uniquely in the tropics include *Bacidiopsis* Kalb, *Crocynia* (Ach.) A. Massal., *Eschatogonia* Trevis., *Krogia* Timdal, *Phyllopsora* Müll. Arg. and *Physcidia* Tuck. Except for *Crocynia*, all are characterized by largely squamulose thalli, with the areoles or squamules often overgrowing a thick prothallus (Fig. 1). This morphology is here termed ‘phyllopsoroid’. Even though *Crocynia* has a more felt-like thallus, we consider this genus also associated with the

100 phylloporoid growthform due to the distinct prothallus. *Phyllopsora* is the largest of these genera and has  
101 been placed in various families, for example Phyllopsoraceae (Hafellner 1984; Elix 2009), Bacidiaceae  
102 (Brako 1989, 1991), and Ramalinaceae (Timdal 2008, 2011). The circumscription of the Phyllopsoraceae  
103 was thereby mainly based on the phylloporoid growth form, which may have evolved independently in  
104 the family as a response to similar ecological conditions (shaded tree trunks in tropical rainforests).  
105 Furthermore, many of these species form vegetative dispersal units such as phyllidia or lacinules that are  
106 rarely found in other temperate genera of the Ramalinaceae. Apart from *Crocynia* and *Phyllopsora*, there  
107 are no published molecular studies or sequences in GenBank for the abovementioned tropical genera.  
108 Hence, the evolution of the phylloporoid growth form has so far not been explored in a phylogenetic  
109 context, nor has the inclusion of all these genera in the Ramalinaceae been confirmed.

110 The aim of this study was to improve the knowledge about phylogenetic relationships and  
111 character evolution in the family Ramalinaceae and to update its classification accordingly. To achieve  
112 this aim, we conducted phylogenetic analyses with multilocus DNA sequence data with a comprehensive  
113 taxon representation. We used ancestral state reconstruction to trace the evolution of morphological  
114 features through time and to explore the two following hypotheses: (1) ellipsoid, simple ascospores are  
115 plesiomorphic in the family; (2) the phylloporoid growth form has evolved repeatedly and independently  
116 from crustose ancestors. Our suggested taxonomic changes to the classification of the family are based on  
117 an integrative approach, abiding by molecular phylogenetic principles while at the same time thoroughly  
118 evaluating morphological characteristics.

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## MATERIALS AND METHODS

**Taxon selection and sampling.**—We obtained sequence data from a large sample of Ramalinaceae representatives, including nearly all type species of genera included in the family by Eriksson & al. (2006), Lumbsch and Huhndorf (2011), Lücking & al. (2017a, b) and Robert & al. (2005). In addition, we included taxa suspected by us to belong in this family based on their morphology as well as members of nominal genera treated as synonyms in Zahlbruckner (1921–1940) and MycoBank. In addition, we included selected members of various families within the Lecanoromycetidae and Umbilicariomycetidae. All specimens were either taken from our own herbaria (O, UPS) or borrowed from other institutions (AAS, ABL, ASU, B, BG, BM, BR, CANB, E, FR, G, GZU, HO, KR, LD, M, MIN, NY, SBBG, SP, TRH, TROM, TSB). Additionally, we downloaded DNA sequences from GenBank. Whenever possible, several species per genus, including the type species, were included. In all, we used DNA sequence data from 175 specimens representing 149 species (Appendix 1). Authorships for genera and species are provided in Appendix 1 and in the Taxonomy chapter, or, for additional taxa, at first mention in the text.

**Morphology and chemistry.**—Selected specimens were subjected to morphological investigations of the thallus and apothecia, ascus analyses and ascospore measurements using light microscopy. Microscope sections were cut on a freezing microtome at 16–20  $\mu\text{m}$  thickness and mounted in water, 10% KOH (K), lactophenol cotton blue and a modified Lugol's solution, in which water was replaced by 50% lactic acid (I). Amyloid reactions were observed in the modified Lugol's solution after pretreatment in K (KI reaction). For identification of lichen substances, we applied thin-layer chromatography (TLC), using the standard methods of Culberson and Kristinsson (1970) and Culberson (1972), modified as suggested by Menlove (1974) and Culberson and Johnson (1982). Examinations were made in the three standard solvent systems A, B' and C.

**Extraction, PCR and sequencing.**—Part of the laboratory work followed the procedure described by Ekman & al. (2008) and Ekman & Blaaid (2011). Other parts used the following approach: Genomic DNA was extracted from apothecia and/or thallus tissue (ca. 1–3 mg) using the E.Z.N.A.® HP Plant DNA Mini Kit (OMEGA Bio-tek, Norcross, Georgia, USA) following the manufacturer's instructions with the modifications described in Bendiksby & Timdal (2013). We selected four nuclear and one mitochondrial genetic marker: the internal transcribed spacer (ITS) region (including ITS1, 5.8S and ITS2) and the downstream large subunit (LSU) of the nuclear ribosomal DNA, the largest subunit of the RNA polymerase II gene (RPB1), the first part of the second largest subunit of the RNA polymerase II gene (RPB2) and the small subunit (mtSSU) of the mitochondrial ribosomal DNA. Polymerase chain reactions (PCR; Table 1) were performed with the primer pairs listed in Table 1. When the first round of amplification was unsuccessful, we applied a nested PCR approach or used internal PCR primers (Table 1). We used half reactions of the Illustra™ PuReTaq Ready-To-Go™ PCR Beads (GE Healthcare, Buckinghamshire, UK), i.e., prior to adding DNA, we transferred 12  $\mu\text{L}$  of the mixture to a new PCR tube. To this, we added 0.5  $\mu\text{L}$  of template DNA for all markers except RPB2, for which we added the double amount of both DNA template (1  $\mu\text{L}$ ) and each primer (2  $\mu\text{L}$ ; 10  $\mu\text{M}$ ). The PCR products were purified with the Illustra™ ExoProStar™ Clean-Up Kit (GE Healthcare, Buckinghamshire, UK) following the manufacturer's instructions, but with a 10-fold enzyme dilution. We used the ABI PRISM® BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Waltham, Massachusetts, USA) for sequencing reactions following the manufacturer's instructions except that the BigDye was diluted four to 10 times for a final 10  $\mu\text{L}$  reaction volume. The respective PCR primers were also used as sequencing primers. We performed a standard ethanol precipitation with EDTA (125 mM), NaOAc (3 M) and 96% ethanol followed by two 70% ethanol washes to clean the final extension PCR products. We added 10  $\mu\text{L}$  of Hi-Di™ Formamide (Applied Biosystems, Waltham, Massachusetts, USA) to the cleaned extension products and subjected them to automatic Sanger sequencing on an ABI PRISM® 3130xl Genetic Analyzer (Applied Biosystems, Waltham, Massachusetts, USA). Alternatively, we sent the purified PCR products to Macrogen Europe (Amsterdam, The Netherlands) for Sanger sequencing according to the company's instructions for sample preparation.

**Sequence Alignment.**—We assembled and edited the resulting sequences using the software Geneious R9 (Kearse & al. 2012). For the separate alignment of the highly variable ITS1 and ITS2 sequences, we used PASTA version 1.7 (Mirarab & al. 2015) with OPAL as aligner and merger, the maximum subproblem set to 50%, RAXML as the tree estimator under a GTR+ $\Gamma$  model and a maximum of 400 iterations. We also used PASTA for the mtSSU alignment with the same settings, except that we used a GTR+I+ $\Gamma$  model to handle potentially invariant sites in conserved regions. As the 5.8S and LSU alignments contain more conserved regions, the online version of MAFFT version 7.313

178 (<http://mafft.cbrc.jp/alignment/software/>; Katoh and Standley 2013) was used (G-INS-i and E-INS-i  
179 algorithms, respectively), with default settings, except that the scoring matrix was set to 20PAM. PASTA  
180 iteratively optimizes the alignment and a maximum likelihood phylogeny, which is an accurate approach  
181 for highly variable datasets, whereas MAFFT produces equally accurate alignment estimations for less  
182 variable datasets in considerably shorter run times than PASTA (Mirarab & al. 2015). For the protein-  
183 coding genes RPB1 and RPB2, we started with the Translation Align option in Geneious R9 (Kearse &  
184 al. 2012) combined with the G-INS-I algorithm and PAM100 scoring matrix of the MAFFT v7 plugin  
185 (Katoh & Standley 2013), and subsequently adjusted resulting alignments manually. Introns were excised  
186 from RPB1; no other data was excluded from the alignments. We trimmed the ends of all resulting  
187 alignments to minimize the amount of terminal missing data.

188 We generated two different alignments: (1) a concatenated alignment containing all five loci but  
189 including only terminals for which at least two loci were represented (altogether 156 terminals, from here  
190 on referred to as 5-locus dataset); and (2) a concatenated mtSSU and ITS alignment which additionally  
191 included taxa for which only one mtSSU or ITS sequence was available (171 terminals, from here on  
192 referred to as 2-locus dataset).

193 **Partitioning and model testing.**—We inferred the best-fitting substitution models and  
194 partitioning scheme for the concatenated 5-locus alignment with PartitionFinder2 (Lanfear & al. 2016),  
195 using the Bayesian Information Criterion (BIC) to select among all possible combinations of models  
196 implemented in MrBayes (1-, 2-, and 6-rate models). Subset rates were treated as proportional ('linked  
197 branch lengths'). We defined 11 potential subsets prior to the analysis: mtSSU, ITS1, 5.8S, ITS2, LSU,  
198 RPB1 codon position (cp) 1, RPB1 cp2, RPB1 cp3, RPB2 cp1, RPB2 cp2 and RPB2 cp3.  
199 PartitionFinder2 suggested that our data be divided into seven subsets, each with the following  
200 substitution model: a GTR+I+ $\Gamma$  model for (1) mtSSU, (2) ITS1 and ITS2, (3) LSU, (4) RPB1 cp1 and  
201 RPB2 cp1, (5) RPB1 cp2 and RPB2 cp2, and a SYM+I+ $\Gamma$  model for (6) 5.8S, and (7) RPB1 cp3 and  
202 RPB2 cp3. The models for the mtSSU and ITS regions as suggested by PartitionFinder2 were also used  
203 for the 2-locus dataset.

204 **Phylogenetic analyses.**—*Boreoplaca ultrafrigida* and *Ropalospora lugubris* were used for rooting  
205 all phylogenies. We checked for incompatibilities among gene trees by subjecting each marker to a  
206 maximum likelihood bootstrap analysis as implemented in RAxML Black Box 8.2.10 (Stamatakis & al.  
207 2008) on the CIPRES webservice (Miller & al. 2010) with default settings. Resulting gene trees were input  
208 to compat.py (Kauff & Lutzoni 2002) using a 75% cut-off for supported incompatibilities.

209 Rogue taxa in the 2-locus alignment were identified using the dropset algorithm suggested by  
210 Pattengale & al. (2011) as implemented in RAxML 8.2.10 (Stamatakis 2014). We excluded three taxa  
211 identified as rogue (i.e., *Myelorrhiza antrea*, *Compsocladium archboldianum*, *Schadonia fecunda*) from  
212 the subsequent 2-locus dataset analyses.

213 Both 5-locus and 2-locus alignments were subjected to maximum likelihood analyses using Garli  
214 2.01 (Zwickl 2006) on the CIPRES webservice (Miller & al. 2010) and on the Abel high performance  
215 computing cluster (University of Oslo, Norway) under the models and partitioning scheme suggested by  
216 PartitionFinder2. We searched for the best tree using 1000 repetitions from a random tree. The  
217 nonparametric bootstrapping analyses included 500 replicates, each on 10 search replicates from a  
218 random tree.

219 We also analysed the datasets phylogenetically using MrBayes 3.2.6 (Ronquist & Huelsenbeck  
220 2003; Altekar & al. 2004) with BEAGLE (Ayres & al. 2012) on the CIPRES webservice (Miller & al.  
221 2010). We used a (1, 1, 1, 1, 1, 1) Dirichlet for the rate matrix, a (1, 1, 1, 1) Dirichlet for the state  
222 frequencies, an exponential (1) distribution for the gamma shape parameter and a uniform (0, 1)  
223 distribution for the proportion of invariable sites. Subset rates were assumed proportional with the prior  
224 distribution following a (1, 1, 1, 1, 1, 1) Dirichlet. We assumed a compound Dirichlet prior on branch  
225 lengths (Rannala & al. 2011; Zhang & al. 2012). For the gamma distribution component of this prior, we  
226 set  $\alpha=1$  and  $\beta=0.05$  (0.04 for the 2-locus alignment), as the expected tree length  $\alpha/\beta$  (taken from the  
227 preceding maximum likelihood analysis) was approximately 21 (26). The Dirichlet component of the  
228 distribution was set to the default (1, 1). Four parallel Markov chain Monte Carlo (MCMC) runs were  
229 performed, each with six chains and the temperature increment parameter set to 0.05 (0.1; Altekar & al.  
230 2004). The appropriate degree of heating, adjusted for swap rates in the interval 0.1–0.7, was determined  
231 by monitoring cold and hot chains in preliminary runs. We used a burnin of 50% and sampled every  
232 10,000th tree. The runs were diagnosed for convergence every  $10^6$  generations and were set to terminate  
233 either at convergence or after having reached  $100 \times 10^6$  generations. Convergence was defined as an  
234 average standard deviation of split frequencies (ASDSF) smaller than 0.01. We projected the bootstrap  
235 support values (BS) from the Garli-analysis onto the MrBayes majority rule consensus tree with posterior

236 probabilities (PP) and collapsed branches with BS < 50 and PP < 0.7. The resulting trees were edited in  
237 TreeGraph 2 (Stöver & Müller 2010).

238 While analyzing our phylogenetic results, we decided to investigate whether a series of specific  
239 phylogenetic hypotheses were within the error margin of the best tree using Shimodairas' Approximately  
240 Unbiased (AU) test (Shimodaira 2002) under maximum likelihood conditions as implemented in IQ-  
241 TREE version 1.6 beta 4 (Nguyen & al. 2015). We used the 5-locus data with the same partitioned model  
242 as in previous analyses. Heuristic searches were carried out for an unconstrained tree as well as the best  
243 (constrained) tree agreeing with each of the null hypotheses. We expanded the default search criteria by  
244 starting each analysis from 1000 parsimony trees (keeping the 100 best), increasing the SPR radius to 10  
245 nodes and checking all NNI swap configurations. The search was stopped after 500 steps without  
246 likelihood score improvement. The AU test was carried out with 10,000 multiscale bootstrap replicates  
247 with a depth of K= 10 (fixed by the software). Hypotheses were rejected if they were less than 5% likely  
248 to be best tree. We also checked for breakdown of asymptotic conditions (Shimodaira 2002: Appendix  
249 10) by testing the residual sums of squares against a chi-square distribution with K-2 degrees of freedom.

250 **Analyses of character evolution.**—We investigated the evolution of selected morphological and  
251 ecological traits by performing character transformation counts as well as reconstruction of ancestral  
252 states. The aim was to test the two following hypotheses on our dataset: (1) ellipsoid, simple spores are  
253 plesiomorphic in the family; (2) the phyllopsoroid growth form has evolved repeatedly and independently  
254 from crustose ancestors. All data manipulation and calculations were carried out in R version 3.4.2 (R  
255 Core Team 2017). We started by coding the following seven morphological traits as discretely valued  
256 characters, either binary or with multiple states: ascospore shape (length:width ratio: 0= ≤3, 1= >3) and  
257 septation (0= none or pseudoseptate, 1= single septate, 2= multiseptate), growth form (0= crustose, 1=  
258 fruticose, 2= foliose, 3= phyllopsoroid), climate preference (0= arctic, 1= temperate, 2= tropical, and 0=  
259 dry, 1= moist), substrate choice (0= soil, 1= rock, 2= bark/wood, 3= living organisms) and the presence of  
260 specialised vegetative dispersal structures, i.e., isidia, lacinules, phyllidia and soredia (0= absent, 1=  
261 present; see Fig. 2). The coding was based on relevant literature (mostly Smith & al. 2009 for the  
262 European taxa, various monographs for the extra-European taxa, e.g., Timdal 1992, Ekman 1996a) and on  
263 our own observations whenever necessary. When the state was unknown for a taxon, we coded the prior  
264 probability as equally divided across all known states. In the next step, we randomly downsampled the  
265 Bayesian posterior tree sample from the 5-locus tree inference to 1000 trees. Taxa not belonging to the  
266 Ramalinaceae were excluded and so were one of the terminals (the one on the longer branch) in all cases  
267 with a species being represented by two terminals. The resulting trees, which preserved the original  
268 branch lengths in number of changes per site, were rooted and are referred to here as our sample of  
269 'phylograms'.

270 Phylograms are desirable if it is assumed that morphological change is proportional to genetic  
271 change. However, applications of ancestral state reconstruction often assume that morphological change  
272 is proportional to time, in which case reconstructions need to be performed on trees with branch lengths  
273 proportional to time ('chronograms'). Litsois & Salamin (2012) and Cusimano & Renner (2014)  
274 demonstrated that reconstructions on phylograms and chronograms, while often similar, can sometimes  
275 give different results. However, to safeguard against results sensitive to the proportionality assumption,  
276 we carried out all reconstructions on phylograms as well as chronograms. Chronograms were generated  
277 from the phylograms using penalized likelihoods under a correlated model as described by Paradis (2013)  
278 with the *chronos()* function of *ape* version 5.0.

279 Stochastic mapping (Nielsen 2002, Huelsenbeck & al. 2003, Bollback 2006) was carried out on  
280 the phylograms and chronograms using the *make.simmap()* function of *phytools* version 0.6.44 (Revell  
281 2012). We simulated 100 character mappings for each of the 1000 trees. For two-state characters, we  
282 applied an asymmetric model that allowed forward and backward rates to be different. For the sake of  
283 minimizing the number of parameters estimated, however, multistate characters (characters with more  
284 than two states) were assumed to follow a symmetric model. In the symmetric model, forward and  
285 backward rates between all pairs of states are assumed equal, whereas these rates can be different between  
286 pairs of states. Simulations were set to use an instantaneous rate matrix, Q, estimated from the empirical  
287 data and a prior distribution of states on the root node estimated from the stationary distribution of Q.  
288 Character transformation counts were subsequently extracted from the sampled maps by using the  
289 *countSimmap()* function and summarized using table summary functions from *matrixStats* version 0.52.2  
290 (Bengtsson 2017) as well as the *HPDinterval()* function of *coda* version 0.19.1 (Plummer & al. 2006). In  
291 addition, we extracted and summarized inferred ancestral states for nodes present in the majority-rule  
292 consensus tree of all mapped trees using the *describe.simmap()* function on two randomly selected maps

293 among the 100 per tree. This downsampling was necessary for reasons of computational time and  
294 memory usage.  
295 Ancestral state reconstructions (ASR) at or near the root node can potentially be influenced by the  
296 assumptions made about the distribution of states at the root. Therefore, we wanted to check for  
297 sensitivity to those assumptions. We did this by use of the *rayDISC()* function of the *corHMM* version  
298 1.22 package (Beaulieu & al. 2013). Reconstructions were made on the extended majority-rule consensus  
299 tree from the Bayesian 5-locus inference and was based on the same character information as in the  
300 stochastic mapping, including distributing unknown states equally across the known states. We performed  
301 marginal reconstructions using three different assumptions about the distribution of states at the root  
302 node: (1) equal distribution of states, (2) the same distribution as in the observed data (Yang 2006: 124),  
303 and (3) estimated from the data and model (Maddison & al. 2007, FitzJohn & al. 2009). The latter setting  
304 most closely resembled the one used in the stochastic mapping.  
305



## RESULTS

**Molecular data.**—Sequences were successfully generated for most of our specimens except for old and/or poor-quality specimens (Appendix 1). In total, we produced 458 new sequences for this study, ranging from 79 to 106 for the various genetic markers (Tables S1, 2). The amplification and sequencing success was highest for mtSSU and ITS, followed by LSU, whereas the amplification of low-copy genes, RPB1 and RPB2, was more challenging. We obtained RPB1 and RPB2 sequences for about 50% of our samples. The 5-locus dataset consisted of 156 taxa and resulted in a 5520 bp long alignment with 2346 parsimony-informative sites and 30.1% missing data (Table 2). The 2-locus dataset of 171 accessions resulted in a 2468 bp long alignment with 974 parsimony-informative sites and 20.9% missing data. Both alignments are available from TreeBase (study no. 22266).

**Phylogenetic analyses.**—Our *compat.py* analyses revealed a few cases of incongruence between individual gene trees, all involving subterminal branches within clades of closely related congeneric species. This incongruence occurred between the (1) mtSSU and RPB1 tree, (2) mtSSU and RPB2 tree, and (3) ITS and RPB1 tree, but affected neither genus delimitations nor deeper branches.

The Bayesian phylogenetic analyses halted automatically after  $15 \times 10^6$  generations for the 5-locus alignment and after  $37 \times 10^6$  generations for the 2-locus alignment, when the ASDSF in the last 50% of each run had fallen below 0.01. We used 3004 (7404 for the 2-locus analysis) trees for constructing the final majority-rule consensus tree. The phylogenetic results generated by Garli and MrBayes showed no incongruences, only varying resolution. The extended majority-rule consensus tree of the 5-locus alignment (Fig. 2), based on the Bayesian topology with all compatible groups ( $BS \geq 50$  and/or  $PP \geq 0.7$ ), showed good resolution and branch support at both genus and species levels. Overall, the 5-locus tree (Fig. 2) was better resolved than the 2-locus tree (Fig. S1). The vast majority of taxa traditionally classified as Ramalinaceae form a well-supported clade (Fig. 2:  $PP = 1$ ,  $BS = 82$ ). The resulting tree from the 2-locus alignment displays the same monophyletic group (Fig. S1:  $PP = 1$ ,  $BS = 60$ ). Among strongly supported clades, eight are considered particularly taxonomically relevant and are indicated to facilitate their discussion (Fig. 2: Ramalinaceae and clades A–G). The genera *Bacidia*, *Bacidina*, *Phyllopsora*, *Physcidia* and *Toninia*, as currently circumscribed, appear non-monophyletic in both the 5- and the 2-locus phylogenies (Figs. 2, S1; notice Fig. 2: A and Fig. S1: B). The following species of genera in the Ramalinaceae fall outside of the family: *Phyllopsora atrocarpa*, *P. lividocarpa*, *P. nigrocincta*, *Toninia squalescens*, and *T. thiopsora*. The following eight genera, currently assigned to the Ramalinaceae, fall outside of the family either based on the clade referred to as Ramalinaceae in our phylogenetic tree (Figs. 2, S1) or based on BLAST searches of generated sequences: *Adelolecia*, *Catinaria*, *Compsocladium*, *Crustospathula*, *Frutidella*, *Japewia*, *Schadonia* and *Tasmidella*. Multiple accessions of species grouped together, except for *Mycobilimbia tetramera*. This situation may have resulted from a misidentification, which, however, does not impair the genus delimitation.

The results of the AU tests rejected ( $p < 0.05$ ) six of our hypotheses and confirmed ( $p > 0.05$ ) the following four hypotheses: *Bacidina* incl. *Woessia*+*Lichingoldia* is monophyletic, *Toniniopsis* is monophyletic, *Toninia*+*Toniniopsis*+*Kiliasia*+*Bibbya*+*Thalloidima* is monophyletic, ‘*Parallopsora*’ (i.e. *Phyllopsora brakoae*, *P. labriformis*, *P. leucophyllina*) is monophyletic (Table 3). The residual sums of squares were all within the lower 95% of a chi-square distribution with eight degrees of freedom, indicating that test conditions were valid.

**Ancestral character states.**—We reconstructed seven ancestral states for the most recent common ancestor (MRCA) of the Ramalinaceae (Fig. 2) as well as for five selected subclades (Fig. 2: C–G). The coding matrix for all coded taxa is provided together with the 5-locus phylogeny (Fig. 2). Median results of the simulations on both phylograms and chronograms show the highest probabilities for the ancestor of the Ramalinaceae to have originated from temperate, moist forests and to have reproduced mainly sexually with long multiseptate ascospores (state probabilities 76–100%; Table 4). Node reconstructions for the five subclades (Fig. 2: C–G) are largely concordant with the Ramalinaceae MRCA apart from the *Ramalina*-group having highest probabilities for 1-septate spores (Table 4). Results of inferences on phylograms and chronograms are mostly similar and both analyses types always recovered the same most probable states. However, differences of up to 22.7 percentage points can be found within the characters ‘Spores’, ‘Climate’ and ‘Vegetative dispersal’ (Table 4). The three priors on the distribution of states at the root node generated similar results (max.  $\pm 5\%$  differences) for the root node as well as five selected subclades (Fig. 2: C–G; Table S1), except for the character ‘Vegetative dispersal’ ( $\pm 30\%$  differences; Table S1). The transformation counts of state changes reveal frequent transitions from short to long spores, from crustose to phylloporoid growth form and from temperate to tropical climate zones (Table 5). Furthermore, the results indicate that it was more common to go from a humid (‘moist’) habitat

364 to a dry one than the reverse (Table 5). Gains as well as losses of vegetative dispersal have been frequent  
365 (Table 5).  
366

## DISCUSSION

In this study, we present the first detailed multi-locus phylogeny of the family Ramalinaceae, including many type species (Fig. 2), and present novel results from ASR analyses on this phylogeny (Tables 4, 5). Most Ramalinaceae genera form a monophyletic clade (Fig. 2: Ramalinaceae; see section on the Ramalinaceae family circumscription). Some genera, however, exhibit varying degrees of non-monophyly, for example *Phyllopsora*, *Physcidia* and *Toninia*. In the current taxonomy, which is mainly based on morphology and apothecial characters, these genera are polyphyletic. Molecular phylogenetic studies – such as the present one – are therefore essential for revealing occurrences of convergent evolution or parallelism within these traditionally morphology-based classifications, and to guide taxonomic genus delimitation. Similar instances of polyphyly can be found throughout several other lichen families and genera (e.g., Divakar & al. 2006; Bendiksby & Timdal 2013; Kirika & al. 2016; Zhao & al. 2016). In our study, we show that phenotypic features, such as the growth form or the presence of a prothallus, are often a result of adaptation to a specific habitat, for example to tropical rainforests, and do not necessarily represent a diagnostic character. In *Phyllopsora*, the ascospore type has proven to be a more reliable taxonomic character at the genus level than the presence and extent of prothallus. In *Toninia*, on the other hand, the pigmentation of the epithecium is of higher taxonomic value. See the respective clade sections for further discussions of each genus.

**Ancestral state reconstruction.**—In our ASR analyses, we used both phylograms and chronograms for reconstruction. Most empirical DNA sequence datasets violate the strict clock assumption (e.g., Ho 2014) indicating that genetic change is often not proportional to time, and there is no obvious reason why morphological change would be different. Hence, we think it is more reasonable to assume that morphological change is proportional to genetic change rather than to time. However, we decided to reconstruct ancestral states on both phylograms and chronograms for comparison, both tree types providing similar transformation counts and state probabilities at nodes (Tables 4, 5). We also tested for sensitivity against assumptions about the state distribution at the root node (Table S1). This test indicates that characters are insensitive to these assumptions, with one distinct exception, viz. vegetative dispersal structures. For that character, assuming an empirical distribution of states at the node (‘Yang’) provides a relatively certain inference that vegetative dispersal structures were absent at the root, whereas other root node assumptions lead to more uncertain inferences. The effect of the varying assumptions at the root has the largest effect on root node inferences but also has some influence on nodes higher up in the tree. Clearly, inferences about the history of vegetative dispersal structures need to be interpreted with care.

According to our overall results from the ASR analyses, the MRCA of the Ramalinaceae most likely evolved in moist temperate forests and reproduced by forming apothecia with long, multiseptate spores (Table 4). Hence, our first hypothesis that simple, ellipsoid spores are plesiomorphic in the family is not supported by the ASR analysis (probability < 14%; Table 4). Extant Ramalinaceae taxa display a wide variety of ascospore types. The phylogenetic sister-family of the Ramalinaceae, the Psoraceae, is a rather small family, which forms mainly ellipsoid and simple spores. This led us to hypothesize the same character state (i.e., ellipsoid, unseptated spores) for the MRCA of the Ramalinaceae, with the different states in ascospore length and septae in extant taxa having evolved repeatedly. Not only do our ASR analyses provide fair support for the long and multiseptate spores in the MRCA of the Ramalinaceae (Table 4), the transformation counts also clearly show a repeated reduction in spore septa and length (Table 5). Apart from reproducing by ascospores, gains as well as losses of vegetative dispersal have generally been frequent (Table 5).

The phylloporoid growth form (Fig. 1) seems to occur exclusively in tropical genera. Both our phylogenetic trees, including mapped character states (Fig. 2) and ASRs (Tables 4, 5), suggest that this growth form developed independently and repeatedly, confirming our second hypothesis. Colonization of the tropical zone from a temperate ancestor as well as from humid (‘moist’) habitats to dry ones has been more common than the reverse (Table 5). Although the Ramalinaceae ancestor apparently arose in temperate forests, tropical genera occur in all major Ramalinaceae clades (Fig. 2: clades C–G). Some species displaying typical phylloporoid growth form, expected to belong in the tropical genus *Phyllopsora*, fell outside the family in the molecular phylogeny (e.g., *P. atrocarpa* or *P. nigrocincta*; Fig. 2: clade A). Moreover, the transformation counts reveal repeated state changes from crustose to phylloporoid growth form, rarely the other way around (Table 5). The evolutionarily flexible nature of this character state on the Ramalinaceae molecular phylogeny (Fig. 2) suggests careful use as a morphological taxon delimitation criterion. This growth form rather seems to be advantageous in tropical moist forests. Lakatos & al. (2006) investigated the growth form of typical corticolous, lowland rainforest

425 lichens and found that the prothallus, which is characteristic for the phylloporoid growth form, serves to  
426 diminish the danger of suprasaturation by rain running down tree stems. A dense prothallus takes up  
427 water like a sponge and keeps the lichen's surface dry enough to ensure an active photosynthesis. Lakatos  
428 & al. (2006) claim that the squamulose growth form results in a larger relative surface area and that the  
429 lichen is hence able to capture more light. Lichens with a phylloporoid growth form can also grow more  
430 easily on irregular surfaces and are more competitive than crustose lichens with the same biomass  
431 (Lakatos & al. 2006). Consequently, these species may grow more easily in the understory of tropical  
432 rainforests. These ecophysiological advantages may explain the high degree of convergent evolution in  
433 the phylloporoid growth form of tropical genera.

434 **Ramalinaceae family circumscription.**—Based on our molecular phylogenetic hypotheses  
435 (Figs. 2, S1), the Ramalinaceae is not monophyletic as currently circumscribed (sensu Lücking & al.  
436 2017a, b). However, most genera and species assigned to the family form a highly supported (PP = 1,  
437 BS = 82), monophyletic clade. We propose this clade as the revised family circumscription for the  
438 Ramalinaceae (Fig. 2: Ramalinaceae). This circumscription is congruent with molecular phylogenetic  
439 results of the Lecanoromycetes produced by Miadlikowska & al. (2014). Their extensive phylogeny  
440 corroborates previous findings by Andersen & Ekman (2005) and Arup & al. (2007) that the genera  
441 *Fruitedella* and *Japewia* do not belong to the Ramalinaceae, as well as Ekman & al.'s (2008) results  
442 showing that the three genera *Adelolecia*, *Catinaria* and *Schadonia* also fall outside of the family. Our  
443 phylogenetic results (Fig. 2) support the exclusion of these five genera from the family and additionally  
444 provide molecular evidence for the exclusion of the genera *Compsocladium*, *Crustospathula* and  
445 *Tasmidella*. Even though we removed *Compsocladium* from the 2-locus dataset because of the outcome  
446 of the rogue taxa analysis, performing BLAST searches of its mtSSU sequence shows high similarity to  
447 taxa within the Lecanorales, mostly from the Pilocarpaceae, but anyway outside of the Ramalinaceae.  
448 Additional DNA sequencing data is necessary to phylogenetically identify its correct taxonomic  
449 placement. *Tasmidella* was, based on morphological investigations, placed in the Megalariaceae by  
450 Kantvilas & al. (1999). The Megalariaceae has since been included in the Ramalinaceae (Ekman 2001).  
451 However, the genus *Tasmidella* clearly does not belong in the Ramalinaceae (Fig. 2). Results from  
452 BLAST searches indicate that it associates with the Lecanoraceae. Detailed phylogenetic studies of  
453 possible close relatives are necessary to determine its correct taxonomic position. The genus  
454 *Crustospathula* was recently placed in the family Malmideaceae based on morphological evidence only  
455 (Cáceres & al. 2017). For a more detailed discussion of *Crustospathula*, see section about clade A. It is  
456 beyond the scope of this study to determine the final taxonomic placement of the excluded genera.

457 On the other hand, we suggest including the genera *Scutula* and *Tylothallia* in the Ramalinaceae  
458 (Figs. 2, S1). *Scutula* was placed in the Ramalinaceae also by Jaklitsch & al. (2016: 127). The affinity of  
459 *Tylothallia* with the Ramalinaceae was revealed already by Ekman (2001) and the molecular phylogeny  
460 by Andersen & Ekman (2005) placed *Scutula* in this family.

461 Ekman (2001) first mentioned the overall anatomical similarities between Ramalinaceae and  
462 Bacidiaceae and suggested synonymization after studying members of both families also in a molecular  
463 context. The previous delimitation of the two families was based on growth form: fruticose and foliose in  
464 Ramalinaceae and crustose lichens in Bacidiaceae. As the two families share anatomical features such as  
465 ascus and ascospore morphology, as well as chemistry, the suggested synonymy was generally quickly  
466 accepted. Lücking & al. (2017a, b) did not mention the Bacidiaceae in their recent classification. Still, the  
467 name Bacidiaceae repeatedly appears in the literature. While Miadlikowska & al. (2014) accept a large  
468 Ramalinaceae, they still indicate the Bacidiaceae (based on the location of the type species) in their  
469 molecular phylogeny, which seemed to receive strong support. Also Sérusiaux & al. (2012), Lendemer &  
470 al. (2016) and McMullin & Lendemer (2016) still accept the Bacidiaceae as a separate family. However,  
471 the 'new' understanding of the Bacidiaceae (sensu Miadlikowska & al. 2014) is not congruent with the  
472 'former' Bacidiaceae (sensu Zahlbruckner 1921–1940), which originally included all crustose taxa, for  
473 example also *Biatora*. Five major clades receive strong support in our molecular phylogeny (Fig. 2:  
474 clades C–G), one of which corresponds to the Bacidiaceae (Fig. 2: C) sensu Miadlikowska & al. (2014).  
475 We therefore continue to synonymize the two families due to their common ascus morphology and the  
476 lack of any consistent diagnostic features that would separate the clades at family level. Both families are  
477 strongly supported as a monophyletic group (Fig. 2) while underlying branches lack consistent  
478 morphological differences to support splitting them up in smaller families. In the following, we discuss in  
479 detail the seven major clades (Fig. 2: A–G) recovered in our analysis, including the two clades (A, B)  
480 falling outside the Ramalinaceae. For details of taxonomic changes, see the Taxonomy chapter.

481 **Clades A and B: excluded species.**—A group of species previously included in the Ramalinaceae  
482 form a strongly supported clade that falls outside of our currently suggested family delimitation (Fig. 2:

483 clade A, PP = 1, BS = 100). Because taxon sampling is scarce outside the Ramalinaceae, it remains  
484 uncertain whether or not all of the species found in clade A are indeed closely related.

485 A standard BLAST search of our DNA sequence data for the Australian species *Psoroma karstenii*  
486 indicates that this species does not belong in the genus *Psoroma*. Elix (1992) excluded the species  
487 together with *P. caesium* from the genus *Psoroma* and suggested transferring them to *Phyllopsora* due to  
488 overall morphological similarities. Our initial morphological investigations suggested placing the two *P.*  
489 *karstenii* specimens close to *Physcidia* due to the overall larger thallus size than found in *Phyllopsora*.  
490 However, our molecular phylogeny clearly indicates that neither *Phyllopsora* nor *Physcidia* is the correct  
491 genus for this species (Figs. 2, S1).

492 The three *Phyllopsora* species, *P. atrocarpa*, *P. lividocarpa* and *P. nigrocincta*, form a strongly  
493 supported group with long branches, indicating that they may be distinct species. Timdal (2008)  
494 mentioned the morphological similarity of *P. atrocarpa* and *P. lividocarpa* as well as the disparity of *P.*  
495 *nigrocincta* from other *Phyllopsora* species. Both *P. atrocarpa* and *P. lividocarpa* produce long, acicular  
496 spores whereas *P. nigrocincta* has ellipsoid to fusiform spores (Timdal 2008). However, all three species  
497 have an overlapping chemistry (Timdal 2008) indicating that they might be closely related. The mtSSU  
498 sequence of the genus *Crustospathula* (Malmideaceae) shows it to form a strongly supported group with  
499 the three *Phyllopsora* species mentioned above (Fig. S1). *Crustospathula* forms stalked soredia (Aptroot  
500 1998), which distinguishes it from the three *Phyllopsora* species. We propose excluding these three  
501 *Phyllopsora* species from the family Ramalinaceae, but more in-depth studies are needed to reveal their  
502 correct taxonomic affiliation and degree of relatedness to each other.

503 *Toninia thiopsora* was excluded from *Toninia* by Timdal (1992) due to deviating paraphyses and  
504 ascus morphology. However, the species was never assigned to a new genus. Our results demonstrate that  
505 *T. thiopsora* does not belong in *Toninia* (Fig. 2: clade A), but further studies are necessary to identify its  
506 closest relatives.

507 It is out of the scope of this study to find the closest relatives to all species in clade A (Fig. 2).  
508 Both the close affinity to *Crustospathula* and GenBank BLAST searches revealed that the three  
509 *Phyllopsora* species, *P. karstenii* and *T. thiopsora* may be members of the Malmideaceae. Our  
510 morphological investigations of the different ascus-structures of the *Phyllopsora*, *Psoroma* and *Toninia*  
511 species, show that they differ strongly from those reported to occur in *Malmidea* by Kalb & al. (2011).  
512 However, recent studies on the Malmideaceae have indicated that the ascus and ascospore structures vary  
513 between the different genera (Cáceres & al. 2017). The family Malmideaceae has lately been investigated  
514 in more detail and several new genera have been described (Cáceres & al. 2017; Muggia & al. 2017;  
515 Sodamuk & al. 2017). Further molecular studies with a dataset including sequences of all known  
516 Malmideaceae genera are necessary to find out whether all species from clade A belong into this family  
517 and whether they form distinct genera.

518 Another *Toninia* species falling out of the Ramalinaceae in our 2-locus phylogenetic hypothesis is  
519 *Toninia squalescens* (Fig. S1: clade B). Timdal (1992) excluded *T. squalescens* from *Toninia* based on  
520 the different paraphyses and asci. In our molecular phylogeny, *T. squalescens* groups together with two  
521 accessions of *Catillaria contristans* in a strongly supported clade (Fig. S1: clade B). BLAST searches of  
522 our mtSSU and ITS sequences of *C. contristans* and *T. squalescens* indicated a high degree of similarity  
523 with species of *Brianaria*, *Micarea*, *Psora* and *Sphaerophorus*. Despite grouping together, *C. contristans*  
524 and *T. squalescens* are morphologically distinct from each other and are not necessarily closely related.  
525 *Toninia squalescens* clearly does not belong in the genus *Toninia* or any of its segregates, but more  
526 detailed analyses are necessary to find its taxonomic affinity. Finally, *C. contristans* is morphologically  
527 very different (e.g., in ascus structure) from members of *Catillaria* s.str. and clearly does not belong in  
528 that genus.

529 **Clade C: *Bacidia*-group.**—The *Bacidia*-group (Fig. 2: clade C) comprises *Bacidia* s.str. in the  
530 sense of Ekman (2001) and includes the type species *Bacidia rosella*. According to our ASR analyses, the  
531 ancestor of this group had character states that were identical to the overall Ramalinaceae MRCA  
532 (Table 4). In addition to *Bacidia*, this clade also comprises the genera *Bacidiopsis* and *Lueckingia* as  
533 well as three species previously referred to *Phyllopsora* and two species previously referred to *Physcidia*.

534 Our phylogeny shows that *Phyllopsora* is highly polyphyletic and can be found in four different  
535 clades (Fig. 2: clades A, C–D, F). The synonymy of *Phyllopsora pertexta* with *Sporacestra prasina* and  
536 *P. borbonica* was indicated by Ekman (1996a) and Timdal (2011). As these species clearly do not belong  
537 in *Phyllopsora* s.str. (Fig. 2: clade F, *Biatora*-group), we resurrect the genus *Sporacestra* for *Phyllopsora*  
538 *pertexta* and related species. The *Physcidia* sp. accession is strongly supported as phylogenetic sister to  
539 the *Sporacestra* clade in our phylogeny. The thallus of the *Physcidia* sp. specimen is large and almost  
540 foliose. However, our current molecular phylogeny shows that growth form is not necessarily a good

541 diagnostic character (Fig. 2). Unfortunately, the *Physcidia* sp. specimen is sterile and consequently  
542 provides no information about apothecium characters, which may be of higher diagnostic value. We  
543 anticipate that this specimen eventually will be placed in a new genus due to its much larger thallus size  
544 and lack of the pronounced prothallus, which contrasts to the minutely areolate *Sporacestra* with a well-  
545 developed prothallus. Additional apotheciate collections of this species should be studied prior to further  
546 evaluating its generic affiliation.

547 The type species of the genus *Bacidiopsora*, *B. squamulosula*, is nested within *Bacidia* s.str. and  
548 should be transferred to *Bacidia*. The close relationship is supported also by the ascospore anatomy, both  
549 having thick-walled, multiseptate ascospores. Already Brako (1991) pointed out that *Bacidiopsora* was  
550 not clearly distinct from *Bacidia*. *Phyllopsora sorediata* was originally described as *Triclinum sorediatum*  
551 by Aptroot & al. (2007), but according to an ongoing study of *Phyllopsora* s.str. by Kistenich & al. (in  
552 prep.), *P. sorediata* does not belong in the genus *Triclinum*. The species contains acicular ascospores like  
553 *Bacidia*, but these are indistinctly (1–) 3-septate unlike most members of *Bacidia*. Given its robust  
554 phylogenetic placement together with *Bacidia* (Fig. 2), we regard *P. sorediata* as better accommodated in  
555 *Bacidia* than in *Phyllopsora* or *Triclinum*, but refrain from formally transferring it to *Bacidia* pending  
556 additional studies at the species level. *Physcidia cylindrophora* is another species found in the strongly  
557 supported *Bacidia*-group (Fig. 2: clade C). This species forms typical lobate thalli of up to 13 cm in  
558 diameter (Kalb & Elix 1995), and does not resemble a *Bacidia* on first sight. However, like *Bacidia* it has  
559 long, multi-septate ascospores and one of the two chemical strains contains the homosekikaic acid  
560 complex (Kalb & Elix 1995) also found in species referred to *Bacidiopsora* as well as in *Bacidia*  
561 *absistens*. While *Bacidia* species typically form a crustose thallus, *Bacidiopsora* species form squamules,  
562 and *P. cylindrophora* is an almost foliose species. However, the ASR analyses indicate that growth form  
563 is flexible and subject to frequent change in an evolutionary perspective (Table 5). Growth form has been  
564 shown to be distributed non-monophyletically across lichen genera and families (e.g., Arup & al. 2013,  
565 Lendemer & Hodkinson 2013). Hence, we accept an extended *Bacidia* s.str. that includes *Bacidiopsora*  
566 and *Physcidia cylindrophora*.

567 The monospecific genus *Lueckingia* is for the first time shown here to belong in the Ramalinaceae  
568 by molecular data. It is the phylogenetic sister to the remaining *Bacidia*-group members and the only  
569 genus with polysporous asci in clade C (Fig. 2). Aptroot & al. (2006) proposed a possible close  
570 relationship with the genus *Physcidia*. However, the type species of *Physcidia* belongs in the *Toninia*-  
571 group (Fig. 2: clade D).

572 **Clade D: *Toninia*-group.**—The *Toninia*-group is a well-supported clade (Fig. 2: clade D, PP = 1,  
573 BS = 87). However, resolution and branch support inside this clade is poor in many instances. Our ASR  
574 analyses of the *Toninia*-group node reveal the ancestor to have character states similar to the  
575 Ramalinaceae ancestor (Table 4). The first shift from corticolous to saxicolous life forms seems to have  
576 taken place during the diversification of *Toninia* s.lat. (Tables 4, 5). The *Toninia*-group comprises the  
577 genera *Aciculopsora*, *Arthrosporium*, *Bacidia*, *Bacidina*, *Eschatogonia*, *Krogia*, *Phyllopsora*, *Physcidia*,  
578 *Scutula*, *Toninia*, and *Waynea*.

579 The tropical genera *Eschatogonia* and *Krogia* are both morphologically readily distinguishable  
580 from other genera. *Eschatogonia* is the only genus in the Ramalinaceae that forms a characteristic  
581 unicellular cortex, while *Krogia* is the only genus forming asci with a nearly non-amyloid tholus and  
582 filiform, curved ascospores that are spirally arranged in the ascus. Our representation of taxa in these two  
583 genera is scarce and it remains to be seen whether they form monophyletic groups.

584 The tropical genus *Physcidia* consists of eight described and one undescribed species, four of  
585 which have been studied here (Appendix 1). Two species, *P. cylindrophora* and *Physcidia* sp., are  
586 phylogenetically placed in the *Bacidia*-group (Fig. 2: clade C), the other two species, *P. wrightii* and *P.*  
587 *striata*, appear in the *Toninia*-group (Fig. S1: clade D). The type species, *P. wrightii*, does not cluster  
588 together with *P. striata* (Fig. S1: clade D). Yet, the poor resolution in Fig. S1 did not unequivocally  
589 exclude the possibility of *P. wrightii* and *P. striata* forming a monophyletic group. *Physcidia striata*  
590 differs from *P. wrightii* by having biatorine apothecia and ellipsoid ascospores (Aptroot & Cáceres 2014).  
591 This might indicate that *P. striata* should not remain in the genus *Physcidia*. Due to the low branch  
592 support and limited taxon sampling of the genus *Physcidia*, we refrain from making taxonomic changes  
593 for *Physcidia*. Increased taxon sampling and more molecular data are needed to address monophyly of  
594 *Physcidia*, after the exclusion of the two species in the *Bacidia*-group (Fig. 2: clade C).

595 Three of the four *Phyllopsora* species occurring in the *Toninia*-group (Fig. 2: clade D), *P. brakoae*,  
596 *P. labriiformis* and *P. leucophyllina*, are phylogenetically unresolved. Their rather diverse thallus  
597 morphology and secondary chemistry do not provide clues to their relationships. The AU test (Table 3),  
598 however, does not reject monophyly of these three species ( $p = 0.2$ ). Hence, we propose the most

599 parsimonious solution of describing the single new genus *Parallopsora* Kistenich, Timdal & Bendiksby  
600 to accommodate *P. brakoeae*, *P. labriformis* and *P. leucophyllina* (Fig. 3b). A fourth *Phyllopsora* species,  
601 *P. lacerata*, falls out in a supported subclade together with *Bacidina* species (Fig. 2), and is therefore  
602 transferred to *Bacidina* (see discussion below). All four *Phyllopsora* species in the *Toninia*-group (Fig. 2:  
603 clade D) differ morphologically from the typical *Phyllopsora* s.str. in the *Biatora*-group (Fig. 2: clade F)  
604 by having longer ascospores and/or forming soredia (cfr. Timdal 2008).

605 We included 13 of the 55 currently accepted species of *Toninia* in our multilocus phylogeny  
606 (Figs. 2, S1) and an additional 16 species in an auxiliary ITS phylogeny (Fig. S2). These include the type  
607 species of the formerly synonymized genera *Bibbya*, *Kiliasia*, *Thalloidima*, and *Toniniopsis*, as well as  
608 *Toninia* s.str. (Figs. 2, S2), which conform, at least partly, with the informal infrageneric arrangement of  
609 *Toninia* proposed by Timdal (1992). Supported subclades of the *Toninia*-group in our multi-locus  
610 molecular phylogeny (Fig. 2: clade D) largely correspond to the same groupings. Moreover, the  
611 monophyly of none of these genera is contradicted in the purely ITS tree (Fig. S2), which has increased  
612 taxon sampling. Timdal (1992) carried out a worldwide taxonomic revision of *Toninia* and excluded  
613 numerous taxa that were morphologically similar but distantly related (mostly outside our current  
614 understanding of the Ramalinaceae). Left in *Toninia* was a core of 48 relatively closely related species, all  
615 terricolous or saxicolous and with weakly conglutinated paraphyses, and many with the squamulose habit  
616 growth form used by Zahlbruckner (1921–1940) to delimit the genus. Our phylogeny (Figs. 2, S1) and  
617 that of Ekman (2001) indicate that numerous species previously treated in *Bacidia*, with a dominance of  
618 corticolous and non-squamulose ones, are more closely related to *Toninia* sensu Timdal (1992) than to  
619 *Bacidia* s.str. The AU tests indicate that splitting *Toninia* is acceptable and so would accepting one large  
620 *Toninia* (as long as *Scutula* is not included; Table 3). However, accepting a single *Toninia* s.lat. would  
621 make it very species-rich and morphologically extremely heterogeneous. Therefore, we prefer to divide  
622 the old *Toninia*, including numerous species currently treated in *Bacidia*, into five genera, all of which are  
623 already described. In the Taxonomy chapter, an additional 15 species are transferred to the five *Toninia*  
624 segregate genera based on overall morphological and anatomical similarity with one or more of the 29  
625 *Toninia* species in Figure S2. Altogether 11 species are left in *Toninia* s.lat., however, pending further  
626 study.

627 The type species of *Toninia*, *T. cinereovirens*, groups together with *T. squalida*, *T. tristis* and  
628 *Arthrosporum popolorum* in a strongly supported clade. This core group of *Toninia* s.str. ('group 2' sensu  
629 Timdal 1992) contains the same kind of green apothecial pigment ('Bacidiagrün', = Bagliettoana-green,  
630 in the terminology of Meyer & Printzen 2000) that can be found in *Arthrosporum* and *Toniniopsis*  
631 (Timdal 1992). Despite having polysporous asci and a corticolous growth form, *Arthrosporum* closely  
632 resembles *Toninia* in other morphological characteristics (Timdal 1992). We therefore propose to include  
633 *Arthrosporum* in the genus *Toninia*. For the remainder of the investigated *Toninia* species, we suggest  
634 resurrecting the genera *Bibbya*, *Kiliasia*, *Thalloidima*, and *Toniniopsis*. The former genus *Bibbya* is  
635 resurrected for *T. bullata*, *T. auriculata*, *T. ruginosa*, as well as for *Bacidia vermifera*, which together  
636 form a strongly supported clade (Figs. 2, S2). These species are characterized by having a reddish brown  
637 pigment (Ruginosa-brown, Meyer & Printzen 2000) and usually long, 3–7-septate ascospores (Timdal  
638 1992; Ekman 1996a). The similarity in pigment composition and ascospore/thallus morphology between  
639 *T. bullata*, *T. ruginosa*, and *T. auriculata* was noted by Timdal (1992), while Ekman (1996a) described  
640 similar characters for *B. vermifera*. *Toninia sculpturata*, *T. philippea*, and *T. athallina* form a supported  
641 clade in our phylogeny that represents the genus *Kiliasia* (Figs. 2, S2). All three species were formerly  
642 placed in the crustose genus *Catillaria* (e.g., by Kilias 1981, 1984) before Hafellner (1984) described  
643 *Kiliasia* and Timdal (1992) later moved them to *Toninia*. Timdal (1992) elaborated on the similarity of  
644 the crustose species *T. philippea* and the cryptothalline species *T. athallina* with 'apparently no diagnostic  
645 anatomical differences between these species' (Timdal 1992: 43). The clade consisting of the three  
646 species *T. candida*, *T. physaroides*, and *T. toniniana* (Fig. 2) corresponds partly to *Thalloidima* (sensu A.  
647 Massal.; i.e., species having 1-septate ascospores) and to *Toninia* 'group 1' and 'group 10' sensu Timdal  
648 (1992; i.e., species having mainly the pigment 'Thalloidimagrün' in the epithecium). In the new  
649 circumscription proposed here, *Thalloidima* contains species that (with few exceptions) have the  
650 characteristic greyish pigment 'Thalloidimagrün' (= Sedifolia-grey, Meyer & Printzen 2000), a thallus  
651 partly or entirely covered by white pruina formed by calcium oxalate, and fusiform, 1-septate ascospores.  
652 The correspondence is not absolute, however, 1-septate ascospores (mainly ellipsoid) also occurring in  
653 *Kiliasia*, *Bibbya*, and *Toninia*, and 'Thalloidimagrün' in *Kiliasia*. The species *T. candida*, *T. physaroides*  
654 and *T. toniniana* are transferred here to *Thalloidima*.

655 The genus *Toniniopsis* was originally described for the single species *T. obscura*, a synonym of  
656 *Bacidia illudens*, and was reduced to synonymy with *Bacidia* by Ekman (1996a). Lücking & al. (2017a,

657 b), however, list it as a separate genus in the Ramalinaceae with *T. obscura* as the type species, and  
658 Timdal (1992) temporarily accepted it as a separate genus from *Toninia* and *Bacidia*. In our 5-locus  
659 phylogeny (Fig. 2), *Toniniopsis obscura* forms a well-supported clade with *Toninia aromatica* and  
660 *Bacidia subincompta*, which appears in the same polytomy as *T. coelestina* and *B. bagliettoana*. An AU  
661 test is unable to reject the possibility that *Toniniopsis*, including all these species, is monophyletic  
662 (Table 3). In addition, *T. verrucarioides* belongs in this genus, as shown by our ITS phylogeny (Fig. S2),  
663 corroborating Ekman (2001). The members of *Toniniopsis*, as understood here, share the presence of a  
664 blue-green pigment in the hymenium and sometimes proper exciple ('Bacidiagrün'; = Bagliettoana-green,  
665 Meyer & Printzen 2000), a red-brown pigment throughout the proper exciple, as well as general  
666 apothecium anatomy. Close relationships between, for example, *T. aromatica*, *T. verrucarioides* and *B.*  
667 *bagliettoana* have previously been pointed out on morphological grounds (Timdal 1992, Ekman 1996a).

668 We included two species of the genus *Scutula*, *S. miliaris*, the type species, and *S. tuberculosa*  
669 (Appendix 1; Fig. S1). We investigated the apothecial structure and ascus morphology of *S. miliaris* and  
670 found the ascus to be extremely similar to *Toninia*. However, the conidial trimorphism found in *Scutula*,  
671 with the macroconidial stage (Karsteniomyces) having oblong to bacilliform conidia, the mesoconidial  
672 stage (Libertiella) bacilliform to falcate conidia, and the microconidial stage bacilliform to filiform  
673 conidia (Triebe & al. 1997), seems to be a distinctive character at the genus level. *Scutula tuberculosa*  
674 and *S. miliaris* form a well-supported clade with *Bacidia circumspecta* as their supported phylogenetic  
675 sister in our 2-locus phylogeny (Fig. S1) and cluster together with *B. auerswaldii* in a strongly supported  
676 clade in the 5-locus phylogeny (Fig. 2). Ekman (1996a) reported three different conidial types for *B.*  
677 *circumspecta* (fusiform to bacilliform, filiform, falcate), whereas *B. auerswaldii* is only known to produce  
678 short-bacilliform conidia (Arvidsson & al. 1988). Upon anatomical reexamination of the aforementioned  
679 *Scutula* and *Bacidia* species, we found them to resemble each other strikingly. The two *Bacidia* species  
680 lack parasitic stages, but a mixture of parasitic (e.g., *T. plumbina*) and non-parasitic species is known to  
681 occur also in *Toninia*. Due to the strong phylogenetic support (Figs. 2, S1) and the morphological  
682 similarities, above all in conidial morphology, we transfer *B. auerswaldii* and *B. circumspecta* to the  
683 genus *Scutula*.

684 The *Toninia*-group (Fig. 2: clade D) also contains four *Bacidina* species, including the type species  
685 *B. phacodes*. However, the four *Bacidina* species do not cluster together. The type species, *B. phacodes*,  
686 forms a well-supported clade with *Bacidia medialis*, *Bacidina brittoniana* and *Phyllopsora lacerata*.  
687 Ekman (2001) suggested moving *B. medialis* into *Bacidina*. *Phyllopsora lacerata* clearly does not belong  
688 to *Phyllopsora* s.str., which phylogenetically falls in the *Biatora*-group (Fig. 2: clade F). *Phyllopsora*  
689 *lacerata* instead shares several morphological characters with members of *Bacidina*, for example the lack  
690 of prothallus and the bacilliform to acicular ascospores (Ekman 1996a, Timdal 2008). Squamulose  
691 species are already known from *Bacidina* (e.g., *B. squamellosa*), despite the majority forming crustose  
692 thalli (Ekman 1996a). Hence, we move *P. lacerata* to *Bacidina*. The remaining two *Bacidina* species in  
693 our tree, *B. inundata* and *B. arnoldiana*, are separated from the core of *Bacidina* s.str. Despite the  
694 apparent non-monophyly on our phylogenetic tree, the AU test does not reject the possibility that these  
695 two species form a monophyletic group with *Bacidia medialis*, *Bacidina brittoniana* and *Phyllopsora*  
696 *lacerata* ( $p = 0.09$ ; Table 3). This result means that our data cannot separate between the possibilities of a  
697 monophyletic and non-monophyletic *Bacidina*. Therefore, we choose the conservative option of retaining  
698 *Bacidina* in the wider sense for the time being. Older genus names for the clade encompassing *B.*  
699 *inundata* and *B. arnoldiana* already exist: *Bacidina sulphurella*, a taxonomic synonym of and the older  
700 name for the nomenclatural type of *Woessia*, *W. fusarioides*, is a close relative of *B. arnoldiana*; *Bacidina*  
701 *inundata*, on the other hand, is a taxonomic synonym of and older name for the nomenclatural type of the  
702 genus, *Lichingoldia*, *L. gyalectiformis* (Ekman 1996b). However, *Woessia* has nomenclatural priority  
703 over *Lichingoldia*.

704 *Bacidia lutescens* was included in our 2-locus phylogeny (Fig. S1), where its position remains  
705 unresolved in the *Toninia*-group. The species has been connected with the Australian genus *Jarmania* by  
706 Palice & al. (2013), mostly because of the presence of lobaric acid in one of the species (Kantvilas 2008).  
707 However, lobaric acid is also present in species of *Biatora* and *Phyllopsora* s.str. (Palice & al. 2013),  
708 which are phylogenetically placed in the *Biatora*-group (Fig. 2: clade F). Moreover, the type of *Jarmania*,  
709 *J. tristis*, has grayanic acid as its major substance (Kantvilas 1996). Unfortunately, we were unable to  
710 generate sequences from our DNA extracts of *Jarmania* and consequently cannot place the genus in our  
711 phylogeny. We therefore refrain from making taxonomic changes, although *B. lutescens* clearly does not  
712 belong in the genus *Bacidia*. Future studies that include DNA sequences of *Jarmania* and further species  
713 within the '*B. lutescens* group' sensu Ekman (1996a) are necessary to draw taxonomic conclusions.



714 *Bacidia incompta* is supported as phylogenetic sister to the remainder of the *Toninia*-group  
715 (Figs. 2, S1: clade D). The difficulty of placing *B. incompta* taxonomically was discussed by Ekman  
716 (2001). The species is characterized by a dark red-brown pigment in the apothecia and pycnidia,  
717 bacilliform ascospores and ellipsoid conidia, traits that together separate it from other genera in the  
718 *Toninia*-group (Fig. 2: clade D). Consequently, we describe the new and monotypic genus *Bellicidia*  
719 Kistenich, Timdal, Bendiksby & S. Ekman to accommodate *B. incompta* (Fig. 3a).

720 **Clade E: *Rolfidium*-group.**—The *Rolfidium*-group forms a small clade comprising, in the  
721 taxonomy prior to this work, representatives of the three genera *Badimia*, *Rolfidium* and *Toninia* (Fig. 2:  
722 clade E, PP = 1, BS = 62). The inferred most probable character states for the MRCA of this group are  
723 identical to those inferred for the MRCA of the Ramalinaceae, i.e., it probably evolved from humid  
724 temperate forests dispersing by long, multiseptate spores and had a crustose growth form (Table 4).

725 The three species *Toninia bumamma*, *T. nigropallida* and *Rolfidium coccocarpioides* form a  
726 strongly supported clade with moderate internal support and with *Badimia dimidiata* as its phylogenetic  
727 sister (Fig. 2). Timdal (1992) excluded both *T. bumamma* and *T. nigropallida* from *Toninia* due to  
728 differences in paraphyses and asci. At the same time, he mentioned the apothecial similarities, which are  
729 also found in *Rolfidium*, between these two species. *Rolfidium coccocarpioides* has previously been  
730 placed in *Toninia* (Zahlbruckner 1921–1940), and Moberg (1986) pointed to the similarities in ascus  
731 morphology between *R. coccocarpioides* and both *Lobiona* (synonym of *Bibhya*) and *Kiliasia*. However,  
732 our molecular phylogeny shows that *Rolfidium* is not closely related to either *Bibhya* or *Kiliasia* (Fig. 2).  
733 We transfer *Toninia bumamma* and *T. nigropallida* to the genus *Rolfidium* because of morphological  
734 similarities and phylogenetic support. Both mtSSU and TLC data showed that the specimen of *Heppsoora*  
735 *indica* (UPS-L-106423) investigated for this study is misidentified *Rolfidium coccocarpioides*. The two  
736 are morphologically highly similar, and Moberg (1986) remarked that the monotypic genus *Heppsoora* is  
737 probably closely related to *Rolfidium*. Sequencing of type material is necessary to find out if *Heppsoora* is  
738 synonymous with *Rolfidium*. If so, the name *Heppsoora* has nomenclatural priority.

739 The foliicolous genus *Badimia* has been placed in various families, for example in the  
740 Pilocarpaceae and Ectolechiaceae due to the presence of campylidia (Lücking & al. 1994), i.e. erect,  
741 helmet-shaped conidiomata. Andersen & Ekman (2005) were the first to investigate the genus with  
742 molecular methods. However, the position of the type species *B. dimidiata* in their phylogeny was not  
743 clear and the species was inferred to belong either in Ramalinaceae or Psoraceae. Our molecular  
744 phylogenetic results provide strong support for including *B. dimidiata* in the Ramalinaceae. Its sister-  
745 group relationship with *Rolfidium*, however, appears less clear.

746 **Clade F: *Biatora*-group.**—The *Biatora*-group (Fig. 2: clade F, PP = 1, BS = 94) almost  
747 exclusively contains crustose lichens mainly from temperate habitats, with apparently only one transition  
748 to the tropics (Fig. 2). This agrees with our ASR results of this clade, which reveal no differences in the  
749 most probable character states of the ancestor of this group compared to those of the Ramalinaceae  
750 MRCA (Table 4). The clade contains members of the tropical genera *Crocynia* and *Phyllopsora*, the  
751 mainly temperate genera *Biatora*, *Bilimbia*, *Mycobilimbia* and *Lecania*, as well as the Antarctic genus  
752 *Thamnolecania*. The species *Catillaria scotinodes* and *Lecidea albohyalina* (Figs. 2, S1) and the genera  
753 *Ivanpisutia*, *Myelorrhiza* and *Myrionora* are also associated with this group (Fig. S1).

754 The genus *Biatora* forms a monophyletic group, albeit weakly supported (PP = 0.9, BS < 50), and  
755 is phylogenetic sister to the strongly supported *Phyllopsora-Crocynia* clade. Our taxon sampling followed  
756 the group delimitation by Printzen (2014). *Myrionora* (Lecanoraceae) was included in the Ramalinaceae  
757 by Palice & al. (2013). *Ivanpisutia* (Lecanorales, *incertae sedis*) on the other hand, has never been  
758 included in the Ramalinaceae, and both are listed as Lecanorales *incertae sedis* by Lücking & al. (2017a,  
759 b). In our 2-locus phylogeny, both appear in supported clades with species of *Biatora* (Fig. S1). The  
760 morphological similarity of *Ivanpisutia oxneri* with *Biatora pacifica* was pointed out by Printzen & al.  
761 (2016). In our phylogeny, *Ivanpisutia* forms a strongly supported clade with *B. ocelliformis*. *Myrionora*  
762 *albidula* was originally described as *B. albidula* and groups here together with *B. ligni-mollis* (Fig. S1).  
763 Consequently, we synonymize both *Ivanpisutia* and *Myrionora* with *Biatora*.

764 Several *Phyllopsora* species fall outside the core group of clades A and C–D (Fig. 2). The type  
765 species of *Phyllopsora*, *P. breviscula*, and the majority of *Phyllopsora* species appear to belong within  
766 the *Biatora*-group (Fig. 2: clade F), forming a strongly supported clade with *Lecidea thaleriza* and the  
767 genus *Crocynia*. *Lecidea thaleriza* was included in *Phyllopsora* by Swinscow and Krog (1981) with  
768 doubt, but was subsequently excluded by Brako (1991). She concluded that *L. thaleriza* ‘belongs to an  
769 undescribed genus in the Bacidiaceae’ (Brako 1991: 58). *Crocynia* has historically been used for lichens  
770 with a cobwebby, non-corticate, felt-like thallus (Plitt 1923). This type of morphology rapidly led to the  
771 assignment of many new species to *Crocynia*: Hue (1924) listed 37 species, while 123 species are listed

772 in GBIF and 169 in MycoBank (both accessed June 2018). Many of these species have since been shown  
773 to belong to other genera and families, for example *Lepraria*. Lücking & al. (2017a, b) list only three  
774 species in their overview for *Crocynia*. The thallus morphology used to characterize *Crocynia* is also  
775 found in a less extreme form in some *Phyllopsora* species, such as in *P. cuyabensis*. Given the  
776 morphological agreement and the nested position of *Crocynia* inside *Phyllopsora* s.str. (Fig. 2: clade F),  
777 we synonymize *Crocynia* with *Phyllopsora*. *Triclinum* is another genus, which has been proposed to be a  
778 synonym of *Phyllopsora* by Tindal (2008). Kistenich & al. (in prep.) investigated several accessions of  
779 *P. cinchonarum*, the type species of *Triclinum*, and found the species to cluster together with other  
780 *Phyllopsora* species. We therefore support the decision of Tindal (2008) to synonymize *Triclinum* with  
781 *Phyllopsora*. As both *Crocynia* (1860), its synonym *Symplocia* (1854), and *Triclinum* (1825) are older  
782 than *Phyllopsora* (1894), we will propose the latter genus name for conservation (Kistenich & al. in  
783 prep.).

784 The Australian genus *Myelorrhiza* is not included in the list of genera in Ramalinaceae in Lücking  
785 & al. (2017a, b). Our sequence of the type species *M. antrea* was excluded from the 2-locus alignment  
786 after a rogue taxon analysis. However, BLAST searches of the mtSSU sequence from *M. antrea* indicate  
787 a close relationship with *Crocynia*. Verdon and Elix (1986) originally postulated an affinity to  
788 *Phyllopsora*, but assigned the genus to Cladoniaceae after additional morphological and anatomical  
789 investigations. The other species in the genus, *M. jenkinsiana*, as well as an unidentified *Myelorrhiza* species  
790 are each represented in GenBank by an 18S rDNA sequence generated in a molecular study on the  
791 Cladoniaceae by Stenroos & al. (2002). The authors show the species to cluster with *Bacidia* and *Toninia*.  
792 However, these were the only two additional species from the Ramalinaceae included in the study.  
793 Further molecular data is required to clarify whether or not a synonymization with *Phyllopsora* is  
794 necessary.

795 The well-supported clade comprising, among others, *Bilimbia*, *Lecania*, *Mycobilimbia*, and  
796 *Thamnolecania* (Figs. 2, S1) is largely concordant with the phylogeny presented by Reese Næsberg & al.  
797 (2007) and Sérusiaux & al. (2010). *Bilimbia*, *Lecania*, and *Mycobilimbia* form well-supported genera.  
798 Sometimes classified as part of a greater *Lecania*, the fruticose genus *Thamnolecania* was considered  
799 problematic by Reese Næsberg & al. (2007) because its circumscription left some species without genus  
800 affiliation in their study. An inclusion of *Thamnolecania* in *Lecania* would require the undesired  
801 inclusion of *Bilimbia* and a morphologically heterogeneous assemblage of species in *Lecania*, which is  
802 why we choose to recognize *Thamnolecania* as a genus. This heterogeneous assemblage of species is  
803 represented by *Catillaria scotinodes* in our phylogeny and further species in the phylogeny of Reese  
804 Næsberg & al. (2007), for example, '*Lecania*' *naegelii*, '*Cliostomum*' *tenerum*, '*Lecidea*' *sphaerella* and  
805 '*Catillaria*' *croatica*. Coppins & al. (1992) excluded *C. scotinodes* from the Catillariaceae on  
806 morphological grounds, noting the similarity with *Toninia*. Reese Næsberg & al. (2007), based on DNA  
807 sequence data, confirmed the association with the Ramalinaceae and suggested a close relationship with  
808 *Bilimbia*, *Lecania* and *Thamnolecania*. Similarly, *Lecidea albohyalina* awaits proper classification. In the  
809 molecular phylogeny of Printzen (2014), *L. albohyalina* is resolved as sister to *Mycobilimbia* and hence  
810 included in *Mycobilimbia* s.lat. Our phylogeny (Fig. 2) corroborates the close relationship with  
811 *Mycobilimbia*. Scarce taxon sampling and the substantial morphological difference between *L.*  
812 *albohyalina* and the otherwise homogeneous *Mycobilimbia* s.str., however, lead us to await further studies  
813 before suggesting a formal reclassification.

814 **Clade G: Ramalina-group.**—The *Ramalina*-group contains the typical fruticose and foliose  
815 macrolichens and additional crustose species (Fig. 2: clade G, PP = 1, BS = 96). The ancestor of the clade  
816 turned out to be similar to the Ramalinaceae MRCA, clearly evolving from a crustose ancestor  
817 (Table S1). However, 1-septate spores seem to be plesiomorphic for this clade (Table S1). The *Ramalina*-  
818 group contained, in the taxonomy prior to this work, the genera *Cenozosia*, *Cliostomum*, *Lopezaria*,  
819 *Megalaria*, *Niebla*, *Ramalina*, *Ramalinopsis*, *Stirtoniella*, *Trichoramalina*, and *Tylothallia*.

820 We confirm the placement of *Stirtoniella* and *Cenozosia* in the Ramalinaceae and present  
821 multilocus sequence data for both genera for the first time. In concordance with the molecular  
822 phylogenetic hypothesis presented by Ekman (2001), *Cliostomum* is the sister group to the genus  
823 *Ramalina*. Lücking & al. (2017a, b) reduced the foliose genus *Ramalinopsis* into synonymy with  
824 *Ramalina* without further explanation. We support this decision due to its nested position within  
825 *Ramalina* (Fig. 2). This is in agreement with the observation that growth form is subject to frequent  
826 change in the Ramalinaceae. The genus *Trichoramalina* was reduced to synonymy with *Ramalina* by  
827 Kashiwadani & Nash (2004). The two species of *Trichoramalina*, *T. crinita* and *T. melanothrix*, were  
828 originally excluded from *Ramalina* due to their characteristic cilia (Rundel & Bowler 1974). The authors,  
829 however, note that morphological characters were overlapping with the genera *Ramalina* and

830 *Desmazieria* (the latter synonymous with *Niebla*). In our molecular phylogeny, the genus *Trichoramalina*  
831 turned out to be polyphyletic: While *T. crinita* is nested within *Ramalina*, *T. melanothrix* forms a strongly  
832 supported clade with *Niebla* (Fig. 2). Both species occur in the same kind of habitat, i.e. semi-arid, coastal  
833 areas with frequent fog formation: *T. crinita* is restricted to southern California and Baja California and *T.*  
834 *melanothrix* to South Africa. It is possible that the characteristic cilia are merely a product of convergent  
835 evolution because of adaptation to similar habitats. In the same way that a dense prothallus can prevent  
836 suprasaturation of lichens in tropical lowland rainforests (Lakatos & al. 2006), cilia might provide the  
837 advantage of condensing water from fog to increase photosynthetic activity during dry periods (Kappen  
838 1988: 59). Cilia should therefore be seen as an adaptation to the habitat rather than a taxonomically useful  
839 character. Another morphological character claimed to discriminate *Trichoramalina* from *Ramalina* is the  
840 presence of black pycnidia (Rundel & Bowler 1974). However, pale pycnidia, similar to those often  
841 found in *Ramalina*, have been observed in *T. crinita*, whereas black pycnidia, similar to those in *Niebla*,  
842 have been observed in *T. melanothrix* (Keuck 1979). The genus *Niebla* generally resembles *Ramalina* and  
843 exhibits extreme plasticity in morphological appearance (Bowler & Marsh 2004). Hence, we accept the  
844 synonymy of *T. crinita* with *Ramalina*, but consider it best to accommodate *T. melanothrix* in *Niebla*  
845 based on both molecular and morphological data.

846 The genus *Megalaria* forms a strongly supported clade in our *Ramalina*-group and includes the  
847 genus *Lopezaria* (Fig. 2). Both *Lopezaria* and *Catillochroma* have been synonymized with *Megalaria* by  
848 Fryday & Lendemer (2010) because of very similar and overlapping morphological characters. However,  
849 Lücking & al. (2011) rejected this synonymization because the type species of those genera are quite  
850 distinct and appear on long branches in a phylogenetic tree with limited taxon sampling (albeit forming a  
851 monophyletic group). In our phylogeny, branches within *Megalaria* s.lat. are also found to be long  
852 (Fig. 2), although not longer than in other parts of the tree thought to represent infrageneric variation  
853 (e.g., *Bacidia*, *Bacidina*). Recognizing *Lopezaria* as a separate genus, however, would orphan *M. laureri*  
854 (a species never proposed to belong to either *Lopezaria* or *Catillochroma*; Fig. 2). We recognize the  
855 shortcoming that no member of *Catillochroma* was included in our study. Given the monophyly of the  
856 group and the apparent absence of morphological characters to distinguish between two or three genera,  
857 we choose to follow Fryday & Lendemer (2010) for the time being and accept a wide circumscription of  
858 *Megalaria* that includes *Catillochroma* and *Lopezaria*.

859 **Genera not investigated.**—Unfortunately, we were not able to sample all genera currently  
860 included in the Ramalinaceae by Lücking & al. (2017a, b). We did not investigate representatives from  
861 the following six genera: *Auriculora*, *Echidnocymbium*, *Hepposora*, *Jarmania*, *Pseudohepatica*, and  
862 *Tibellia*. The specimens were either too valuable to sample destructively for DNA (e.g., *Hepposora indica*)  
863 or did not amplify with PCR (e.g., *Jarmania tristis*, *Pseudohepatica* sp.), potentially due to fragmented  
864 DNA or development of PCR-inhibitory substances in old fungarium specimens. Clearly, there is a need  
865 for improved methods to obtain high-quality DNA from old and/or poor specimens. High-throughput  
866 sequencing methods might hold the key to successfully sequencing fragmented DNA in the future. Until  
867 further molecular or morphological evidence becomes available, we recommend treating these genera as  
868 recognized members of the Ramalinaceae.

869

870 **TAXONOMIC TREATMENT**

871

872 Revised taxonomy of the family Ramalinaceae including accepted names and their basionyms, names  
873 used in our figures and tables as well as important synonyms:

874

875 °: Not studied molecularly

876 \*: Studied sequence(s) of one or more included, non-type species

877 \*\*: Studied sequence(s) of the type species

878 \*\*\*: Studied sequence(s) of type specimen of the type species

879

880

881 *Aciculopsora* Aptroot & Trest\*\*\* in Aptroot & al., J. Hattori Bot. Lab. 100: 618. 2006. – Type:

882 *Aciculopsora salmonea* Aptroot & Trest (holotype).

883

884 *Auriculora* Kalb°, Lichenes Neotrop. 10: 2. 1988. – Type: *Auriculora byssomorpha* (Nyl.) Kalb

885 (holotype) [≡ *Lecidea byssomorpha* Nyl.].

886

887 *Bacidia* De Not.\*\*, Giorn. Bot. Ital. 2: 189. 1846. – Type: *Bacidia rosella* (Pers.) De Not. (lectotype

888 designated by Clements & Shear 1931: 119) [≡ *Lichen rosellus* Pers.].

889 = *Byssopsora* A. Massal.°, Mem. Reale Ist. Veneto Sc.: 89. 1861. – Type: *Byssopsora stupposa*

890 A. Massal. (holotype) [≡ *Bacidia stupposa* (A. Massal.) Zahlbr.].

891 = *Psorella* Müll. Arg.\*\*, Bull. Herb. Boissier 2, append. 1: 11. 1894. – Type: *Psorella*

892 *pannaroidea* (C. Knight) Müll. Arg. (lectotype designated by Clements & Shear 1931: 319) [≡ *Bacidia*

893 *pannaroidea* C. Knight; = *Bacidia wellingtonii* (Stirt.) D.J. Galloway].

894 = *Megalopsora* Vain.\*\*, Ann. Acad. Sci. Fenn., Ser. A, 15, 6: 27. 1921. – Type: *Megalopsora*

895 *cylindrophora* (Taylor) Vain. (lectotype designated by Clements & Shear 1931: 322) [≡ *Physcidia*

896 *cylindrophora* (Taylor) Hue; = *Bacidia cylindrophora* (Taylor) Kistenich, Timdal, Bendiksby & S.

897 Ekman; = *Parmelia cylindrophora* Taylor].

898 = *Bacidiomyces* Cif. & Tomas.°, Atti Ist. Bot. Lab. Crittog. Univ. Pavia 10: 39, 65. 1953, nom.

899 illeg. (Art. 52.1, superfluous name for *Bacidia*). – Type: *Bacidiomyces rubellae* Cif. & Tomas., nom.

900 illeg. (holotype) [≡ *Bacidia rubella* (Hoffm.) A. Massal.].

901 = *Bacidiopsora* Kalb\*\*, Lichenes Neotrop. 10: 4. 1988. – Type: *Bacidiopsora squamulosula*

902 (Nyl.) Kalb (holotype) [≡ *Bacidia squamulosula* (Nyl.) Zahlbr.; *Lecidea squamulosula* Nyl.].

903 *Notes.* – Ekman (1996a: 36) attempted a morphological circumscription of *Bacidia* that included

904 species referred here to *Bibhya*, *Scutula*, *Toninia*, and *Toniniopsis*. In the revised circumscription, the

905 genus includes species with acicular ascospores, pycnidia with filiform and curved conidia, and a proper

906 exciple consisting of furcate hyphae with very thin cell lumina and thick, heavily gelatinized cell walls

907 (terminal cells sometimes excepted). In addition, cell lumina are thinner and cell walls thicker in the old

908 (lower) part of the exciple than in the younger (upper) part.

909

910 *Bacidia cylindrophora* (Taylor) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824363] =

911 *Parmelia cylindrophora* Taylor, London J. Bot. 6: 165. 1847. – Lectotype (designated by Kalb &

912 Elix 1995: 284): India. Madras, *C. Wright* (BM, not seen).

913

914 *Bacidina* Vězda\*\*, Folia Geobot. Phytotax. 25: 431. 1991, nom. cons. – Type: *Bacidina phacodes*

915 (Körb.) Vězda (holotype) [≡ *Bacidia phacodes* Körb.].

916 = *Woessia* D. Hawksw. & Poelt°, Pl. Syst. Evol. 154: 207. 1986, nom. rej. – Type: *Woessia*

917 *fusarioides* D. Hawksw., Poelt & Tscherm.–Woess [= *Bacidina sulphurella* (Samp.) M. Hauck & V.

918 Wirth].

919 = *Lichingoldia* D. Hawksw. & Poelt\*\*, Pl. Syst. Evol. 154: 203. 1986, nom. rej. – Type:

920 *Lichingoldia gyalectiformis* D. Hawksw. & Poelt [= *Bacidina inundata* (Fr.) Vězda].

921 *Notes.* – The genus *Bacidina* is treated here in a wide sense to include *Woessia* and *Lichingoldia*,

922 because of morphological similarities and because the AU test (Table 3) indicates that the best tree in

923 which *Bacidina* in this sense forms a single monophyletic group is not significantly different from the

924 overall best tree. Despite a vast increase in the amount of data, this is the exact same situation reported by

925 Ekman (2001). *Bacidina* is represented here by the type species *B. phacodes* (Körb.) Vězda as well as *B.*

926 *arnoldiana* (Körb.) V. Wirth & Vězda, *B. brittoniana* (Riddle) LaGreca & S. Ekman (treated as *B. varia*

927 S. Ekman by Ekman 1996a), *B. inundata* (Fr.) Vězda, *B. lacerata* (Timdal) Kistenich, Timdal, Bendiksby

928 & S. Ekman, and *B. medialis* (Tuck. ex Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman. *Bacidina* is  
929 characterized by the wide excipular cell lumina (causing what is sometimes referred to as a  
930 paraplechtenchymatous exciple) that tend to become wider with age (the gelatinized cell walls more or  
931 less maintaining their thickness). With the inclusion of *Bacidina lacerata*, overall thallus morphology in  
932 the genus is extended to include forms with up to 1 mm wide squamules. Species forming smaller  
933 squamules are known from before, for example *B. squamellosa* S. Ekman and *B. neosquamulosa* (Aptroot  
934 & Herk) S. Ekman. The ‘*Woessia*’ group, represented here by *B. inundata* and *B. arnoldiana*, differs  
935 somewhat from the type species of *Bacidina* and its relatives in often having a more distinctly  
936 paraplechtenchymatous exciple to the point where individual hyphae are difficult to follow from the inner  
937 part of the exciple to the edge. Furthermore, filiform, curved and non- or few-septate conidia are the rule  
938 in *Woessia*, whereas *B. phacodes* and relatives mostly have straight or moderately curved conidia with  
939 multiple septa. In the end, *Woessia* may very well turn out to constitute a separate genus from *Bacidina*,  
940 but this requires further investigation.

941  
942 ***Bacidina lacerata*** (Timdal) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824364] ≡  
943 *Phyllopsora lacerata* Timdal, Lichenologist 39: 352. 2008. – Holotype: Peru. Loreto, Reserva  
944 Nacional Allpahuayo Mishana, within a 2.3 km distance from Centro de Investigaciones  
945 Allpahuayo, N of the road, site 19, 3°57.31'S, 73°25.46'W, alt. 120–50 m, tree trunk in rainforest,  
946 2006, *E. Timdal 10213* (O L-144583!).

947  
948 ***Bacidina medialis*** (Tuck. ex Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824494]  
949 ≡ *Lecidea medialis* Tuck. ex Nyl. in Triana & Planchon, Ann. Sci. Nat., Bot., Ser. 4, 19: 346.  
950 1863. ≡ *Bacidia medialis* (Tuck. ex Nyl.) de Lesd., Bryologist 24: 68. 1921. – Lectotype  
951 (designated by Ekman 1996: 86): Nicaragua, *C. Wright* (H-NYL 17372 specimen c!).

952  
953 ***Badimia*** Vězda\*\*, Folia Geobot. Phytotax. 21: 206. 1986. – Type: *Badimia dimidiata* (Leight.) Vězda  
954 (holotype) [≡ *Lecanora dimidiata* Leight.].

955  
956 ***Bellicidia*** Kistenich, Timdal, Bendiksby & S. Ekman\*\*, **gen. nov.** [MB824445]. – Type: *Bellicidia*  
957 *incompta* (Borrer) Kistenich, Timdal, Bendiksby & S. Ekman. Fig. 3a.  
958 *Etymology.* – Based on the concatenation of *bellus* and the ending *-cidia* from its former  
959 placement in *Bacidia*. The Latin word *bellus* means ‘pretty’ and is meant to balance the somewhat  
960 disparaging epithet given to the only known species, derived from *incomptus* and meaning ‘plain’.  
961 *Description.* – *Thallus* crustose coarsely granular with confluent granules, grey-green to grass-  
962 green to brown-green, indeterminate. Prothallus not present. Upper cortex a false cortex (‘Scheinrinde’)  
963 sensu Poelt (1958). Lower cortex lacking. Photobiont a unicellular green alga. *Ascomata* apothecia,  
964 biatorine, black, mostly flat but sometimes becoming convex, with distinct, shiny margin, often irregular  
965 in shape, adnate to thallus. Proper exciple and hypothecium dark red-brown (K+ purplish). Hymenium  
966 colourless or with faint red-brown pigment below, but young asci often surrounded by a gelatinous cap  
967 with red-brown pigment. Paraphyses simple or sparingly branched above; apices not or only narrowly  
968 clavate. Asci octosporous, clavate. Ascospores bacilliform, straight or only slightly curved, 15–30 µm  
969 long and 1.5–2 µm wide, with (1–) 3 (–5) thin septa. *Conidiomata* pycnidia, black, more or less immersed  
970 in thallus, unilocular, up to ca. 0.2 mm wide, with dark red-brown (K+ purplish) pigment. Conidiophores  
971 lining pycnidial cavity, forming conidia terminally. Conidia more or less ellipsoid, 5–9 µm long and 2–  
972 2.5 µm wide, non-septate or sometimes with a single septum.

973 *Chemistry.* – No secondary substances.

974 *Notes.* – *Bellicidia incompta* appears in a solitary position on a branch as sister to the rest of the  
975 *Toninia* clade (Fig. 2). The branch uniting the group has strong support and so has the sister branch to  
976 *Bellicidia*. Morphologically, *Bellicidia* stands out by its combination of dark red-brown pigment in the  
977 apothecia and pycnidial wall, bacilliform ascospores and prominent pycnidia with ellipsoid conidia.

978  
979 ***Bellicidia incompta*** (Borrer) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824446] ≡  
980 *Lecidea incompta* Borrer in Hooker & Sowerby, Suppl. Engl. Bot. 2: tab. 2699. 1831 ≡ *Bacidia*  
981 *incompta* (Borrer) Anzi, Cat. Lich. Sondr. 70. 1860. – Syntypes: United Kingdom, England,  
982 marked “E.B.S.”, W. Borrer (BM974478, not seen; UPS L-906205!).

983  
984 ***Biatora*** Fr.\*\*, Lichenum Dianome Nova: 7. 1817, Fr. non Ach. – Type: *Biatora vernalis* (L.) Fr.  
985 (lectotype designated by Clements & Shear 1931: 319) [≡ *Lichen vernalis* L.].

- 986 = *Myrionora* R.C. Harris\*\* in Harris & al., *Evansia* 5: 27. 1988. – Type: *Myrionora albidula*  
987 (Willey) R.C. Harris (holotype) [= *Biatora albidula* Willey].  
988 = *Ivanpisutia* S.Y. Kondr., Lökös & Hur\*\*, *Acta Bot. Hung.* 57: 97. 2015. – Type: *Ivanpisutia*  
989 *oxneri* S.Y. Kondr., Lökös & Hur, *Acta Bot. Hung.* 57: 100. 2015 (holotype) [= *Biatora oxneri* (S.Y.  
990 Kondr., Lökös & Hur) Printzen & Kistenich].  
991  
992 ***Biatora oxneri*** (S.Y. Kondr., Lökös & Hur) Printzen & Kistenich, **comb. nov.** [MB 824365] =  
993 *Ivanpisutia oxneri* S.Y. Kondr., Lökös & Hur, *Acta Bot. Hung.* 57: 100. 2015. – Holotype: Russia.  
994 Far Eastern Federal District, Khasan District, along the pass to the second Golden Stream, along  
995 the Kamenisty stream, 43.115278°N, 131.518889°E, deciduous forest, on bark of deciduous tree,  
996 2013, S.Y. Kondratyuk et al. *RU-13* (herb. KolRI 020233, not seen).  
997  
998 ***Bibbya*** J.H. Willis\*\*, *Victorian Naturalist* 73: 125. 1956. – Type: *Bibbya muelleri* (F. Wilson) J.H. Willis  
999 (holotype) [= *Toninia bullata* (Meyen & Flot.) Zahlbr.].  
1000 = *Lobiona* H. Kiliás & Gotth. Schneid.\*\*, *Lichenologist* 10: 27. 1978. – Type: *Lobiona*  
1001 *albomarginata* H. Kiliás & Gotth. Schneider (holotype) [= *Toninia auriculata* Timdal].  
1002 *Notes.* – This genus was included in *Toninia* by Timdal (1992) and corresponds to his species  
1003 groups 4 and 8 and partly group 5. We also include a species previously placed in *Bacidia*.  
1004 Morphologically, this genus is characterized by a reddish brown, K+ red pigment (‘Ruginosa-brown’, in  
1005 the terminology of Meyer & Printzen 2000) in the apothecium and rim of the exciple. The thallus varies  
1006 from crustose to squamulose or bullate and the ascospores from ellipsoid, 1-septate to filiform,  
1007 pluriseptate.  
1008 According to our molecular phylogeny (Figs. 2, S2), the following species belong in the genus:  
1009 *Bibbya albomarginata* (H. Kiliás & Gotth. Schneid.) Kistenich, Timdal, Bendiksby & S. Ekman, , *B.*  
1010 *bullata* (Meyen & Flot.) Kistenich, Timdal, Bendiksby & S. Ekman, , *B. lutosa* (Ach.) Kistenich, Timdal,  
1011 Bendiksby & S. Ekman, , *B. ruginosa* (Tuck.) Kistenich, Timdal, Bendiksby & S. Ekman, , and *B.*  
1012 *vermifera* (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman.  
1013 The following species and subspecies are included here in *Bibbya* because of morphological  
1014 similarities with one or more of the species listed above, even though DNA sequences are not available:  
1015 *Bibbya australis* (Timdal) Timdal, *B. austroafricana* (Timdal) Timdal, *B. glaucocarpa* (Timdal) Timdal,  
1016 *B. hosseusiana* (Gyeln.) Timdal, *B. ruginosa* ssp. *pacifica* (Timdal) Timdal, and *B. subcircumspecta*  
1017 (Coppins) S. Ekman.  
1018  
1019 ***Bibbya albomarginata*** (H. Kiliás & Gotth. Schneid.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb.**  
1020 **nov.** [MB 824366] = *Lobiona albomarginata* H. Kiliás & Gotth. Schneid., *Lichenologist* 10: 27.  
1021 1978. = *Toninia auriculata* Timdal, *Opera Bot.* 110: 44. 1992. – Holotype: Peru. Huanuco, Stadt  
1022 Huanuco, Hügel am Stadtrand, Erde, alt. 1950 m, 1973, E. Hegewald & P. Hegewald (GZU!).  
1023  
1024 ***Bibbya australis*** (Timdal) Timdal, **comb. nov.** [MB 824371] = *Toninia australis* Timdal, *Opera Bot.* 110:  
1025 45. 1992. – Holotype: Australia. South Australia, between Waikirie and Blanchetown, poorly  
1026 developed soil crusts in opened-up mallee, 1967, W.A. Weber & D. McVean L-47162 (COLO!).  
1027  
1028 ***Bibbya austroafricana*** (Timdal) Timdal, **comb. nov.** [MB 824372] = *Toninia austroafricana* Timdal,  
1029 *Opera Bot.* 110: 47. 1992. – Holotype: Leshoto. Div. Qachas Nek, Mokhotlong, bank of a stream,  
1030 on dolorite, 1963, L. Kofler (LD!).  
1031  
1032 ***Bibbya bullata*** (Meyen & Flot.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824367] =  
1033 *Lecidea bullata* Meyen & Flot., *Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur.* 19, Suppl. 1:  
1034 227. 1843. = *Toninia bullata* (Meyen & Flot.) Zahlbr., *Beih. Bot. Zentralbl.* 19, 2: 76. 1905. –  
1035 Lectotype (designated by Timdal 1992: 48): Chile/Peru. Peruvia, ad Tacoram, terricola, G. Meyen  
1036 (G!).  
1037  
1038 ***Bibbya glaucocarpa*** (Timdal) Timdal, **comb. nov.** [MB 824373] = *Toninia glaucocarpa* Timdal, *Opera*  
1039 *Bot.* 110: 63. 1992. – Holotype: Australia. Australian Capital Territory, Paddy’s River, a tributary  
1040 of the Cotter, W of Canberra, on limestone outcrops, 1968, W.A. Weber & L.G. Adams L-49550  
1041 (COLO!).  
1042

- 1043 **Bibhya hosseusiana** (Gyeln.) Timdal, **comb. nov.** [MB 824374] ≡ *Toninia hosseusiana* Gyeln., Ann.  
 1044 Hist.-Nat. Mus. Natl. Hung. 35: 98. 1942. – Holotype: Argentina. Córdoba, La Calera Sud, 1933,  
 1045 C.C. *Hosseus* 213 (BP!).  
 1046
- 1047 **Bibhya lutosa** (Ach.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824368] ≡ *Lecidea*  
 1048 *lutosa* Ach., Lichenogr. Universalis: 182. 1810. ≡ *Toninia lutosa* (Ach.) Timdal, Opera Bot 110:  
 1049 69.1992. – Holotype: Switzerland. ‘Helvetia’, s. coll. (H-ACH 299A!).  
 1050
- 1051 **Bibhya ruginosa** (Tuck.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824369] ≡  
 1052 *Lecidea ruginosa* Tuck., Lich. Calif.: 26. 1866. ≡ *Toninia ruginosa* (Tuck.) Herre., Proc. Wash.  
 1053 Acad. Sci. 12: 103. 1910. – Lectotype (designated by Lamb 1954: 144): USA. California, Oakland  
 1054 Hills, serpentine rocks, *H.N. Bolander 102* (FH-TUCK!).  
 1055
- 1056 **Bibhya ruginosa** ssp. *pacifica* (Timdal) Timdal, **comb. nov.** [MB 824375] ≡ *Toninia ruginosa* ssp.  
 1057 *pacifica* Timdal, Opera Bot. 110: 90. 1992. – Holotype: USA. California, Santa Barbara Co., Santa  
 1058 Cruz Island, W end of the island, on the rim of the “Trailer Barranca”, in rock crevices, 1986, W.A.  
 1059 Weber & C. Bratt [Weber, Lich. Exs. COLO No 663], (COLO!).  
 1060
- 1061 **Bibhya subcircumspecta** (Coppins) S. Ekman, **comb. nov.** [MB 824406] ≡ *Bacidia subcircumspecta*  
 1062 Coppins, Lichenologist 24: 351. 1992. – Holotype: UK. Caledonia, Mid Ebudes (V.C.103), Mull,  
 1063 Tobermory, Upper Druimfin, on lignum of *Pinus* trunk, 1968, P.W. James (BM, not seen).  
 1064
- 1065 **Bibhya vermifera** (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824370] ≡ *Lecidea*  
 1066 *vermifera* Nyl., Bot. Not. 1853: 98. 1853. ≡ *Bacidia vermifera* (Nyl.) Th. Fr., Lichenogr. Scand.  
 1067 1(2): 363. 1874. – Lectotype (designated by Ekman 1996: 110): Sweden. Holmiae (Marieberg), ad  
 1068 quercus, W. Nylander (H-NYL 17507!).  
 1069
- 1070 **Bilimbia** De Not.\*\* Giorn. Bot. Ital. 2: 190. 1846. – Type: *Bilimbia hexamera* De Not. (lectotype  
 1071 designated by Timdal 1992: 24; non Fink 1910: 85, Art. 10.5) [= *Bilimbia sabuletorum* (Schreb.)  
 1072 Arnold].  
 1073 ≡ *Weitenwebera* Opiz\*\*, Lotos 7: 235. 1857, non Opiz 1839, nom. nov. pro *Bilimbia* De Not.,  
 1074 nom. illeg. (Art. 52.1, 53.1 ). – Type: the type of *Bilimbia* De Not.  
 1075 = *Myxobilimbia* Hafellner\*\*, Stapfia 76: 154. 2001. – Type: *Myxobilimbia lobulata* (Sommerf.)  
 1076 Hafellner (holotype) [≡ *Bilimbia lobulata* (Sommerf.) Hafellner & Coppins; ≡ *Lecidea lobulata*  
 1077 Sommerf.].  
 1078
- 1079 **Cenozosia** A. Massal.\*\* Neagen. Lichenum: 4. 1854. – Type: *Cenozosia inanis* (Mont.) A. Massal.  
 1080 (holotype) [≡ *Ramalina inanis* Mont.].  
 1081
- 1082 **Cliostomum** Fr.\*\* Syst. Orb. Veg. 1: 116. 1825. – Type: *Cliostomum corrugatum* (Ach.) Fr. (holotype)  
 1083 [≡ *Lecidea corrugata* Ach.].  
 1084 ≡ *Rhytismella* P. Karst.\*\* Hedwigia 23: 60. 1884, nom. illeg. (Art. 52.1, superfluous name for  
 1085 *Cliostomum* Fr.). – Type: *Rhytismella corrugata* (Ach.) P. Karst. (holotype) [≡ *Cliostomum corrugatum*  
 1086 (Ach.) Fr.; ≡ *Lecidea corrugata* Ach.].  
 1087 = *Sporoblastia* Trevis.\* Nuovi Ann. Sci. Nat. Rendiconti Sess. Soc. Agrar., Ser. 3, 3: 460. 1851. –  
 1088 Type: *Sporoblastia griffithii* (Sm.) Trevis. (lectotype designated by Hafellner 1984: 268) [≡ *Cliostomum*  
 1089 *griffithii* (Sm.) Coppins; ≡ *Lichen griffithii* Sm.].  
 1090
- 1091 **Eschatogonia** Trevis.\*\* Spighe e Paglie: 6. 1853. – Type: *Eschatogonia montagnei* Trevis. (holotype) [  
 1092 ≡ *Eschatogonia prolifera* (Mont.) R. Sant.; ≡ *Biatora prolifera* Mont.].  
 1093
- 1094 **Echidnocymbium** Brusse°, Mycotaxon 29: 173. 1987. – Type: *Echidnocymbium speciosum* Brusse  
 1095 (holotype).  
 1096
- 1097 **Heppsora** D.D. Awasthi & Kr.P. Singh°, Bryologist 80: 537. 1977. – Type: *Heppsora indica* D.D.  
 1098 Awasthi & Kr.P. Singh (holotype).  
 1099
- 1100 **Jarmania** Kantvilas°, Lichenologist 28: 230. 1996. – Type: *Jarmania tristis* Kantvilas (holotype).

- 1101  
 1102 ***Kiliasia*** Hafellner\*\*, Beih. Nova Hedwigia 79: 261. 1984. – Type: *Kiliasia athallina* (Hepp) Hafellner  
 1103 (holotype) [= *Toninia athallina* (Hepp) Timdal; ≡ *Biatora athallina* Hepp].  
 1104 Notes. – This genus was included in *Toninia* by Timdal (1992) and includes species from his  
 1105 groups 1, 3, and 7. Morphologically, this genus is characterized by a more or less crustose thallus,  
 1106 although both non-lichenized and squamulose species occur. The ascospores vary from ellipsoid, 1-  
 1107 septate to shortly bacilliform, 3-septate.  
 1108 According to our molecular phylogeny (Figs. 2, S2), the following species belong in the genus:  
 1109 *Kiliasia athallina* (Hepp) Hafellner, *K. nordlandica* (Th. Fr.) Kistenich, Timdal, Bendiksby & S. Ekman,  
 1110 *K. pennina* (Schaer.) Kistenich, Timdal, Bendiksby & S. Ekman, *K. philippea* (Mont.) Hafellner, and *K.*  
 1111 *sculpturata* (H. Magn.) Kistenich, Timdal, Bendiksby & S. Ekman.  
 1112 The following species are included here in *Kiliasia* because of morphological similarities with one  
 1113 or more of the species listed above, even though DNA sequences are not available: *Kiliasia episema*  
 1114 (Nyl.) Hafellner, *K. granulosa* (Szatala) Timdal, *K. superioris* (Timdal) Timdal, and *K. tristis* (Müll.  
 1115 Arg.) Hafellner.  
 1116  
 1117 ***Kiliasia granulosa*** (Szatala) Timdal, **comb. nov.** [MB 824379] ≡ *Thalloidima granulorum* Szatala, Ann.  
 1118 Hist.-Nat. Mus. Natl. Hung., n. Ser. 5: 132. 1954. ≡ *Toninia weberi* Timdal, Opera Bot. 110: 118.  
 1119 1992. – Holotype: Iran. Semnān, Montes Elburs orient., Firukuh, saxa calc., 1948, *K.H. Rechinger*  
 1120 & *F. Rechinger* (W!).  
 1121  
 1122 ***Kiliasia nordlandica*** (Th. Fr.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824376] ≡  
 1123 *Toninia nordlandica* Th. Fr., Lichenogr. Scand. 1(2): 339. 1874. – Holotype: Norway. Nordland,  
 1124 Gildeskål, ad praedium Indyr, *J.M. Norman* (UPS!).  
 1125  
 1126 ***Kiliasia pennina*** (Schaer.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824377] ≡  
 1127 *Lecidea pennina* Schaer., Lich. Helv. Spic. (3): 120. 1828. ≡ *Toninia pennina* (Schaer.) Gyeln.,  
 1128 Lilloa 3: 52. 1938. – Neotype (designated by Timdal 1992: 77): Switzerland. Zürich, an  
 1129 Alpenfindlingen, *s. coll.* [Hepp, Flechten Eur. No 238] (G!).  
 1130  
 1131 ***Kiliasia sculpturata*** (H. Magn.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824378] ≡  
 1132 *Catillaria sculpturata* H. Magn., Lich. Cent. Asia: 66. 1940. ≡ *Toninia sculpturata* (H. Magn.)  
 1133 Timdal, Opera Bot. 110: 92. 1992. – Holotype: China. Gansu, Yü-her-hung, alt. 2700–2800 m,  
 1134 1932, *B. Bohlin 80* (S!).  
 1135  
 1136 ***Kiliasia superioris*** (Timdal) Timdal, **comb. nov.** [MB 824380] ≡ *Toninia superioris* Timdal, Opera Bot.  
 1137 110: 103. 1992. – USA. Michigan, Keweenaw Co., Isle Royale National Park, Edwards Island at  
 1138 NE end of Tobin Harbor, in balsam fir woods along rock cliffs and on upper shore at NE tip of  
 1139 island, 1983, *C.M. Wetmore 48492* (MIN!).  
 1140  
 1141 ***Krogia*** Timdal\*\*\*, Lichenologist 34: 293. 2002. – Type: *Krogia coralloides* Timdal (holotype).  
 1142  
 1143 ***Lecania*** A. Massal.\*\*, Alc. Gen. Lich.: 12. 1853. – Type: *Lecania fuscella* (Schaer.) A. Massal.  
 1144 (holotype) [= *Parmelia pallida* var. *fuscella* Schaer.].  
 1145 = *Bayrhofferia* Trevis.\*\*, Rivista Period. Lav. Regia Accad. Sci. Lett. Arti Padova 5: 69. 1857. –  
 1146 Type: *Bayrhofferia spadicea* (Flot.) Trevis. (**lectotype designated here**) [= *Lecania spadicea* (Flot)  
 1147 Zahlbr. ≡ *Lecanora spadicea* Flot. – Lectotype (designated by Mayrhofer 1988: 93): Italy. Apulien,  
 1148 Brindisi, Isola Petagne, 1847, *G.L. Rabenhorst* (L, not seen)].  
 1149 = *Dimerospora* Th. Fr.\*\*, Lich. Arct.: 97. 1860. – Type: *Dimerospora aipospila* (Wahlenb.) Th.  
 1150 Fr. (holotype) [= *Lecania aipospila* (Wahlenb.) Th. Fr.; ≡ *Parmelia aipospila* Wahlenb.].  
 1151 = *Lecaniella* Jatta\*\*, Monogr. Lich. Ital. Merid.: 142. 1889. – Type: *Lecaniella cyrtella* (Ach.)  
 1152 Jatta (lectotype designated by Hafellner 1984: 289) [= *Lecania cyrtella* (Ach.) Th. Fr.; ≡ *Lecidea cyrtella*  
 1153 Ach.].  
 1154 = *Adermatis* Clem.\*\*, Gen. Fung.: 79, 175. 1909. – Type: *Adermatis nylanderiana* (A. Massal.)  
 1155 Clem. (holotype) [= *Lecania nylanderiana* A. Massal.].  
 1156 = *Dyslecanis* Clem.\*\*, Gen. Fung.: 79, 175. 1909. – Type: *Dyslecanis syringeae* (Ach.) Clem.  
 1157 (holotype) [= *Lecania fuscella* (Schaer.) A. Massal.; ≡ *Parmelia pallida* var. *fuscella* Schaer.].  
 1158



- 1159 **Lueckingia** Aptroot & L. Umaña\*\*\* in Aptroot & al., J. Hattori Bot. Lab. 100: 619. 2006. – Type:  
 1160 *Lueckingia polyspora* Aptroot & L. Umaña (holotype).  
 1161
- 1162 **Megalaria** Hafellner\*\*, Beih. Nova Hedwigia 79: 302. 1984. – Type: *Megalaria grossa* (Nyl.) Hafellner  
 1163 (holotype) [= *Lecidea grossa* Nyl.].  
 1164 = *Lopezaria* Kalb & Hafellner\*\*, in Kalb, Lichenes Neotrop. 11: 2. 1990. – Type: *Lopezaria*  
 1165 *versicolor* (Flot.) Kalb & Hafellner [= *Megalaria versicolor* (Flot.) Fryday & Lendemer; = *Heterothecium*  
 1166 *versicolor* Flot.].  
 1167 = *Catillochroma* Kalb°, Biblioth. Lichenol. 95: 298. 2007. – Type: *Catillochroma endochroma*  
 1168 (Fée) Kalb (holotype) [= *Megalaria endochroma* (Fée) Fryday & Lendemer; = *Lecanora endochroma*  
 1169 Fée].  
 1170
- 1171 **Mycobilimbia** Rehm\*\*, Rabenh. Krypt.-Fl., Ed. 2, 1, 3: 295, 327. 1889. – Type: *Mycobilimbia obscurata*  
 1172 (Sommerf.) Rehm (lectotype designated by Clements & Shear 1931: 315) [= *Lecidea spheroides*  
 1173 var. *obscurata* Sommerf.; = *Mycobilimbia tetramera* (De Not.) Hafellner & Türk].  
 1174 = *Probilimbia* Vain.\*\*, Természetrázi Fü. 22: 318. 1899, nom. nov. pro *Mycobilimbia* Rehm,  
 1175 nom. illeg. (Art. 52.1). – Type: the type of *Mycobilimbia*.  
 1176
- 1177 **Myelorrhiza** Verdon & Elix\*\*\*, Brunonia 9: 194. 1986. – Type: *Myelorrhiza antrea* Verdon & Elix  
 1178 (holotype).  
 1179 *Note.* – The genus may be close to, or a synonym of, *Phyllopsora*, see Discussion above.  
 1180
- 1181 **Niebla** Rundel & Bowler\*\*, Mycotaxon 6: 497. 1978, nom. nov. pro *Desmazieria* Mont. – Type: the type  
 1182 of *Desmazieria*.  
 1183 = *Desmazieria* Mont.\*\*, Ann. Sci. Nat., Bot., Ser. 3, 18: 303. 1852, non Dumontier 1822, nom.  
 1184 illeg. (Art. 54.1). – Type: *Desmazieria homalea* (Ach.) Mont. (holotype) [= *Niebla homalea* (Ach.)  
 1185 Rundel & Bowler; = *Ramalina homalea* Ach.].  
 1186 = *Vermilacinia* Spjut & Hale\*\* in Spjut, Flechten Follmann (Daniëls & al., eds): 345. 1995. –  
 1187 Type: *Vermilacinia combeoides* (Nyl.) Spjut & Hale (holotype) [= *Niebla combeoides* (Nyl.) Rundel &  
 1188 Bowler; = *Ramalina combeoides* Nyl.].  
 1189 *Notes.* – *Trichoramalina melanothrix* (Laurer) Rundel & Bowler is the sister taxon of *Niebla* in  
 1190 our phylogeny (Fig. 2) and seems to be better accommodated in *Niebla* than in *Ramalina*; see Discussion  
 1191 above. Hence, we make the new combination *Niebla melanothrix* (Laurer) Kistenich, Timdal, Bendiksby  
 1192 & S. Ekman.  
 1193
- 1194 ***Niebla melanothrix*** (Laurer) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824407] =  
 1195 *Ramalina melanothrix* Laurer in Nylander, Syn. Meth. Lich. 1(2): 290. 1860. – Isotypes: South  
 1196 Africa. Cap, s. coll. (O L-189956!), Cap B. Spei, *J.F. Drège* (H-NYL 37197, not seen).  
 1197
- 1198 ***Parallopsora*** Kistenich, Timdal & Bendiksby\*\*, **gen. nov.** [MB 824439] – Type: *Parallopsora*  
 1199 *leucophyllina* (Nyl.) Kistenich, Timdal & Bendiksby. Fig. 3b.  
 1200 *Etymology.* – Based on the concatenation of *para-* (by the side of, near) and *-llopsora* (from the  
 1201 three included species' former placement in *Phyllopsora*).  
 1202 *Description.* – *Thallus* squamulose, effuse, mainly geotropically arranged or forming circular thalli  
 1203 with radiating marginal lobes; squamules up to 2 mm wide, adnate when young, soon ascending, more or  
 1204 less imbricate; upper side pale green to bluish green, glabrous to finely tomentose; soralia present or  
 1205 absent; prothallus absent. Upper cortex composed of thick-walled, irregularly oriented hyphae with  
 1206 angular to shortly cylindrical lumina, 10–35 µm thick, lacking an epinecral layer, not containing crystals.  
 1207 Photobiont unicellular green algae. Medulla containing lichen substances or not, KI–. Lower cortex  
 1208 lacking. *Ascomata* apothecia, biatorine, up to 1.0 mm diam., weakly convex, with an indistinct and more  
 1209 or less disappearing margin, brown, dull, epruinose, not pubescent along the margin. Proper excipulum  
 1210 composed of radiating, conglutinated, thick-walled hyphae with thread-like lumina; hypothecium not  
 1211 distinctly delimited from excipulum, pale brown to colourless, chondroid, composed of irregularly  
 1212 oriented, thick-walled hyphae with cylindrical to thread-like lumina; hymenium colourless or faintly  
 1213 yellow, with amyloid gelatin, ca. 40 µm high; paraphyses conglutinated, straight, simple or rarely  
 1214 branched, ca. 2 µm wide, with a slightly swollen, colourless apical cell; ascus clavate, up to 30 × 8 µm,  
 1215 with a well-developed, amyloid tholus often with a small ocular chamber and with an axial mass in lower

1216 part or extending through the tholus (*Bacidia*-type), octosporous; ascospores bacilliform to acicular,  
1217 simple or with indistinct pseudosepta, colourless, not halonate. *Conidiomata* not seen.  
1218 *Chemistry*. – Homosekikaic acid, sekikaic acid, methyl-barbatate, or no lichen substances.  
1219 *Notes*. – According to our phylogeny (Fig. 2), two more *Phyllopsora* species appear in this clade  
1220 and belong in *Parallopsora*: *P. brakoae* (Timdal) Kistenich, Timdal & Bendiksby and *P. labriformis*  
1221 (Timdal) Kistenich, Timdal & Bendiksby.  
1222  
1223 ***Parallopsora brakoae*** (Timdal) Kistenich, Timdal & Bendiksby, **comb. nov.** [MB 824442] ≡  
1224 *Phyllopsora brakoae* Timdal, Lichenologist 40: 343. 2008. – Holotype: Peru. Loreto, Reserva  
1225 Nacional Allpahuayo Mishana, within a 2.3 km distance from Centro de Investigaciones  
1226 Allpahuayo, N of the road, site 43, 3°58.48'S, 73°25.86'W, alt. 120–150 m, tree trunk in rainforest,  
1227 "bosque de varillal seco", 2006, *E. Timdal 10253* (O L-144623!).  
1228  
1229 ***Parallopsora labriformis*** (Timdal) Kistenich, Timdal & Bendiksby, **comb. nov.** [MB 824443] ≡  
1230 *Phyllopsora labriformis* Timdal, Lichenologist 40: 350. 2008. – Holotype: Peru. Loreto, Jenaro  
1231 Herrera, within a 3.6 km distance from the Research Center, N of the road, site 112, 4°53.93'S,  
1232 73°83.91'W, alt. 120–150 m, tree trunk in rainforest, 2006, *E. Timdal 10419* (O L-144789!).  
1233  
1234 ***Parallopsora leucophyllina*** (Nyl.) Kistenich, Timdal & Bendiksby, **comb. nov.** [MB 824441] ≡ *Lecidea*  
1235 *leucophyllina* Nyl. in Triana & Planchon, Ann. Sci. Nat., Bot., Ser. 4, 19: 347. 1863. ≡  
1236 *Phyllopsora leucophyllina* (Nyl.) Timdal, Lichenologist 40: 352. 2008. – Holotype: Cuba. S. loc.,  
1237 *C. Wright* (H-NYL 17345c,e!).  
1238  
1239 ***Phyllopsora*** Müll. Arg.\*\*\*, Bull. Herb. Boissier 2, append. 1: 11. 1894. – Type: *Phyllopsora breviuscula*  
1240 (Nyl.) Müll. Arg. (lectotype designated by Clements & Shear 1931: 319) [≡ *Lecidea breviuscula*  
1241 Nyl.].  
1242 = *Triclinum* Fée\*\*, Essai Crypt. Écorc.: 147, Pl. 33, Fig. 4. 1825. – Type: *Triclinum cinchonarum*  
1243 Fée (holotype) [≡ *Phyllopsora cinchonarum* (Fée) Timdal].  
1244 = *Symplocia* A. Massal.\*\*, Neagen. Lich.: 4. 1854, nom. rej. vs *Crocynia* (Ach.) A. Massal. –  
1245 Type: *Symplocia gossypina* (Sw.) A. Massal. (holotype) [≡ *Phyllopsora gossypina* (Sw.) Kistenich,  
1246 Timdal, Bendiksby & S. Ekman; ≡ *Lichen gossypinus* Sw.].  
1247 = *Crocynia* (Ach.) A. Massal.\*\*, Atti Reale Ist. Veneto Sci. Lett. Arti, ser. 3, 5: 251. 1860, nom.  
1248 cons. vs *Symplocia* A. Massal. ≡ *Lecidea* sect. *Crocynia* Ach., Lichenogr. Universalis: 217. 1810; type:  
1249 *Crocynia gossypina* (Sw.) A. Massal. (holotype) [≡ *Phyllopsora gossypina* (Sw.) Kistenich, Timdal,  
1250 Bendiksby & S. Ekman; ≡ *Lichen gossypinus* Sw.].  
1251 = *Squamacidia* Brako\*\*, Mycotaxon 35: 6. 1989. – Type: *Squamacidia janeirensis* (Müll. Arg.)  
1252 Brako (holotype) [≡ *Thalloidima janeirensis* Müll. Arg.; = *Phyllopsora cinchonarum* (Fée) Timdal].  
1253 *Notes*. – The circumscription of *Phyllopsora* proposed here differs markedly from that proposed  
1254 by Swinscow & Krog (1981) and modified by Timdal (2008). The new circumscription is based on our  
1255 molecular phylogeny (Fig. 2), which places *Phyllopsora* in a sister position to *Biatora*. *Phyllopsora*  
1256 differs morphologically from *Biatora* mainly in forming larger thallus elements, usually squamules, and  
1257 in being attached to a generally more felty hypothallus. Printzen (1995) discussed the morphological  
1258 differences between the two genera and, based on chemistry, shape of conidiospores and apothecial  
1259 anatomy, assumed that the genera are closely related. All *Phyllopsora* species studied so far having  
1260 soredia and/or acicular to filiform ascospores are now excluded from the genus. We exclude 10 species  
1261 and place them in the genera *Bacidia*, *Bacidina*, *Parallopsora*, *Sporacestra* and an unnamed genus. We  
1262 include two species that were previously placed in *Crocynia* and one in *Lecidea*, together with eight  
1263 studied *Phyllopsora* species, in the newly circumscribed genus *Phyllopsora*. Still, ca. 50 species of  
1264 *Phyllopsora* remain to be studied with molecular methods.  
1265 The name *Phyllopsora* is antedated by *Triclinum*, *Symplocia* and *Crocynia*, but will be proposed  
1266 for conservation (Kistenich & al. in prep.).  
1267 According to our molecular phylogeny (Fig. 2), at least one more *Crocynia* species belongs in  
1268 *Phyllopsora*: *Phyllopsora pyxinoides* (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman.  
1269  
1270 ***Phyllopsora gossypina*** (Sw.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824408] ≡  
1271 *Lichen gossypinus* Sw., Prodr.: 146. 1788. ≡ *Crocynia gossypina* (Sw.) A. Massal., Atti Reale Ist.  
1272 Veneto Sci. Lett. Arti, ser. 3, 5: 252. 1860. – Syntypes: Jamaica. 1784-1786, *O. Swartz* (UPS L-  
1273 000259!, UPS L-134473!).

- 1274  
 1275 ***Phyllopsora pyxinoides*** (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824409] ≡  
 1276 *Crocynia pyxinoides* Nyl., Sert. Lich. Trop: 37. 1891. – Holotype: Cuba. “In ins. Cuba”, *C. Wright*  
 1277 [Wright, Lich. Cub. Ser. 2, No. 145] (H-NYL 22059, not seen).  
 1278
- 1279 ***Physcidia*** Tuck.\*\*, Proc. Amer. Acad. Arts 5: 399. 1862. – Type: *Physcidia wrightii* (Tuck.) Tuck.  
 1280 (lectotype designated by Clements & Shear 1931: 322) [≡ *Physcia wrightii* Tuck.].  
 1281 ≡ *Psoromopsis* Nyl. 1869\*\*, Syn. Meth. Lich. 2: 56. 1863, nom. inval. (Art. 36.1a). – Type:  
 1282 *Psoromopsis wrightii* (Tuck.) Nyl. (holotype) [≡ *Physcidia wrightii* (Tuck.) Tuck.; ≡ *Physcia wrightii*  
 1283 Tuck.].  
 1284 ?= *Callopis* (Müll. Arg.) Gyeln.°, Acta Fauna Fl. Universali, Ser. 2, Bot. 1, 5–6: 8. 1933. ≡  
 1285 *Physcidia* sect. *Callopis* Müll. Arg., Jahrb. Königl. Bot. Gart. Berlin 2: 314. 1883. – Type: *Physcidia*  
 1286 *callopis* (Meyen & Flot.) Müll. Arg. (holotype) [≡ *Lecanora callopis* Meyen & Flot.].  
 1287 *Notes.* – Eight species are currently included in *Physcidia* (Kalb & Elix 1995, Aptroot & Cáceres  
 1288 2014) and an additional, apparently undescribed species is included in this study as *Physcidia* sp. Four  
 1289 species were included in our molecular phylogeny (Figs. 2, S1) and they do not form a monophyletic  
 1290 group. The type species, *P. wrightii*, and *P. striata* Aptroot & al. are placed in the *Toninia*-group (Fig. S1:  
 1291 clade D), but low branch support in this part of the tree makes it impossible to conclude whether they are  
 1292 congeneric or not. *Physcidia cylindrophora* and *P. sp.*, however, are placed in the *Bacidia*-group (Fig. 2:  
 1293 clade C), the former nested within *Bacidia* and the latter as the sister to *Sporacestra*. The growth form of  
 1294 *Physcidia*, i.e., large, almost foliose squamules on a hypothallus, has clearly evolved repeatedly in the  
 1295 Ramalinaceae, even in the genus *Bacidia*. *Physcidia cylindrophora* is transferred here to *Bacidia*, but  
 1296 *Physcidia* sp. may either be included in *Sporacestra* or in a new genus pending further studies. The two  
 1297 species *P. cylindrophora* and *P. striata* differ from the other species of *Physcidia* in having biatorine, not  
 1298 lecanorine, apothecia, and *P. striata* also differs in having ellipsoid, not bacilliform to filiform,  
 1299 ascospores.  
 1300
- 1301 ***Pseudohepatica*** P.M. Jørg.°, Bryologist 96: 435. 1993. – Type: *Pseudohepatica pachyderma* P.M.Jørg.  
 1302 (holotype).  
 1303
- 1304 ***Ramalina*** Ach.\*\*, in Luyken, Tent. Hist. Lich.: 95. 1809. – Type: *Ramalina fraxinea* (L.) Ach. (typ.  
 1305 cons.) [≡ *Lichen fraxineus* L.].  
 1306 ≡ *Ramalinomyces* Cif. & Tomas.\*\*, Atti Ist. Bot. Lab. Crittog. Univ. Pavia 10: 44, 70. 1953, nom.  
 1307 illeg. (Art. 52.1, superfluous name for *Ramalina*); type: *Ramalinomyces fraxineae* Cif. & Tomas., nom.  
 1308 illeg. [≡ *Ramalina fraxinea* (L.) Ach.; ≡ *Lichen fraxineus* L.].  
 1309 ?= *Platysma* Hill°, Gener. Nat. Hist., Ed. 2, 2: 88. 1773, nom. illeg., non *Platysma* P. Browne ex  
 1310 Adans. 1763. – Type: not designated.  
 1311 = *Chlorodictyon* J. Agardh°, Öfvers. Kongl. Vetensk.-Akad. Förh. 27: 433. 1870. – Type:  
 1312 *Chlorodictyon foliosum* J. Agardh [= *Ramalina menziesii* Taylor].  
 1313 ?= *Alectoriopsis* Elenkin°, Izv. Glavn. Bot. Sada S.S.S.R. 28: 292. 1929. – Type: not designated.  
 1314 = *Dievernia* M. Choisy°, Bull. Soc. Bot. France 78: 455. 1931. ≡ *Ramalina* subgen. *Euramalina*  
 1315 sect. *Tenuicorticatae* subsect. *Solidae* Du Rietz, Svensk Bot. Tidskr. 20: 298. 1926. – Type: *Ramalina*  
 1316 *evernioides* Nyl. (holotype) [= *Ramalina maciformis* (Delise) Bory].  
 1317 = *Ramalinopsis* (Zahlbr.) Follmann & Huneck\*\*, Willdenowia 5: 211. 1969. ≡ *Ramalina* sect.  
 1318 *Ramalinopsis* Zahlbr. in Magnusson & Zahlbruckner, Ark. Bot. 32A, 2: 4. 1945. – Type: *Ramalina*  
 1319 *mannii* Tuck. (holotype) [≡ *Ramalinopsis mannii* (Tuck.) Follmann & Huneck].  
 1320 = *Trichoramalina* Rundel & Bowler\*\*, Bryologist 77: 191. 1974. – Type: *Trichoramalina crinita*  
 1321 (Tuck.) Rundel & Bowler (holotype) [≡ *Ramalina crinita* Tuck.].  
 1322 = *Fistulariella* Bowler & Rundel\*\*, Mycotaxon 6: 195. 1977. ≡ *Ramalina stirps* *Fistularia* Vain.,  
 1323 Acta Soc. Fauna Fl. Fenn. 7: 14. 1890. – Type: *Ramalina inflata* (Hook. f. & Taylor) Hook. f. & Taylor  
 1324 (lectotype designated by Bowler & Rundel 1977: 195) [≡ *Cetraria inflata* Hook. f. & Taylor].  
 1325
- 1326 ***Rolfidium*** Moberg\*\*, Lichenologist 18: 305. 1986. – Type: *Rolfidium peltatum* Moberg (holotype) [=   
 1327 *Rolfidium coccocarpioides* (Nyl.) Timdal].  
 1328 *Notes.* – According to our molecular phylogeny (Fig. 2), the following species belong in this  
 1329 formerly monotypic genus: *Rolfidium bumammum* (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman and  
 1330 *R. nigropallidum* (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman  
 1331

- 1332 **Rolfidium bumammum** (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824411] ≡  
1333 *Lecidea bumamma* Nyl. in Crombie, J. Linn. Soc., Bot. 15: 177. 1876. ≡ *Toninia bumamma* (Nyl.)  
1334 Zahlbr., Cat. Lich. Univ. 4: 263. 1926. – Holotype: South Africa. Western Cape, Cap. B. Spei,  
1335 1874, A.E. Eaton (H-NYL 16843!).  
1336
- 1337 **Rolfidium nigropallidum** (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824412] ≡  
1338 *Lecidea nigropallida* Nyl. in Hue, Nouv. Arch. Mus. Hist. Nat., Ser. 3, 3: 124. 1891. ≡ *Toninia*  
1339 *nigropallida* (Nyl.) Abbayes, Bull. Inst. Franç. Afrique Noire, A., 17: 982. 1955. – Holotype:  
1340 South Africa. Western Cape, Cap. B. Spei, *J.F. Drège 9286* (H-NYL 19645!).  
1341
- 1342 **Scutula** Tul.\*\*, Ann. Sci. Nat., Bot., Ser. 3, 17: 118. 1852, nom. cons., non Lour. – Type: icon of *Scutula*  
1343 *wallrothii* Tul. in Tulasne, Ann. Sci. Nat., Bot., Ser. 3, 17: tab. 14, fig. 14–24, 1852 (typ. cons.) [= *Scutula*  
1344 *miliaris* (Wallr.) Trevis.].  
1345 = *Hollosia* Gyeln.\*\*, Borbásia 1: 153. 1939. – Type: *Hollosia vertesensis* Gyeln. (holotype) [= *Scutula*  
1346 *epiblastematica* (Wallr.) Rehm].  
1347 = *Karsteniomyces* D. Hawksw.\*\*, Trans. Brit. Mycol. Soc. 74: 371. 1980. – Type: *Karsteniomyces*  
1348 *peltigerae* (P. Karst.) D. Hawksw. (holotype) [= *Stagonopsis peltigerae* P. Karst.] [anamorph of *Scutula*].  
1349 Notes. – *Scutula* was treated by Triebel & al. (1997) and Wedin & al. (2007) to include a set of  
1350 lichenicolous species. The association with Ramalinaceae was first made by Andersen & Ekman (2005)  
1351 and is confirmed here (Fig. S1). We expand *Scutula* here to include lichen-forming species without any  
1352 obvious parasitic life-cycle stages. The parasitic members of *Scutula* are known to produce two or three  
1353 types of pycnidia containing either micro-, meso- or macroconidia. Similarly, '*Bacidia*' *circumspecta*  
1354 produces three pycnidial types (Ekman 1996a), whereas '*B.*' *auerswaldii* is only known to produce short-  
1355 bacilliform conidia (described by Arvidsson & al. 1988) that are likely to correspond to the microconidia  
1356 in *Scutula*. Two new combinations are necessary: *Scutula circumspecta* (Vain.) Kistenich, Timdal,  
1357 Bendiksby & S. Ekman and *S. effusa* (Rabenh.) Kistenich, Timdal, Bendiksby & S. Ekman.  
1358
- 1359 **Scutula circumspecta** (Vain.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824488] ≡  
1360 *Lecidea bacillifera* var. *circumspecta* Nyl. ex Vain., Meddeland. Soc. Fauna Fl. Fenn. 10: 22.  
1361 1883. ≡ *Lecidea circumspecta* (Vain.) Hedl., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 18, 3(3):  
1362 71. 1892. ≡ *Bacidia circumspecta* (Vain.) Malme, Bot. Not. 1895: 140. 1895. – Lectotype  
1363 (selected by Ekman 1996: 69): Finland. Tavastia australis, Lammi, Evo, 1874, *J.P. Norrlin*  
1364 [Norrlin & Nylander, Herb. Lich. Fenn. No. 185] (H!).  
1365
- 1366 **Scutula effusa** (Rabenh.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824489] ≡  
1367 *Bilimbia effusa* Rabenh., Rabenhorst: Lich. Eur. Exs. 32. 1855. ≡ *Bacidia effusa* (Rabenh.) Lettau,  
1368 Hedwigia 52: 132. 1912, nom. illeg., non (Sm.) Trevisan 1856. ≡ *Lecidea auerswaldii* Stizenb.,  
1369 Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1880/81: 416. 1882. ≡ *Bacidia auerswaldii* (Stizenb.)  
1370 Mig., Krypt.-Fl. Deutschl. 4, 2: 267. 1931. – Lectotype (selected by Ekman 1996: 66): Germany.  
1371 Leipzig, an einer alten Ulme in Rosenthal, 1855, *B. Auerswald* [Rabenhorst, Lich. Eur. Exs. No.  
1372 32] (W!).  
1373
- 1374 **Sporacestra** A. Massal.\*\*, Atti Reale Ist. Veneto Sci. Lett. Arti, Ser. 3, 5: 264. 1860. – Type: *Biatora*  
1375 *prasina* Mont. & Tuck., non (Fr.) Fr. (holotype) [= *Sporacestra pertexta* (Nyl.) Stapnes &  
1376 Timdal].  
1377 Notes. – *Sporacestra* consists of one or two species that were previously placed in *Phyllopsora*  
1378 (Timdal & Krog 2001, Timdal 2011).  
1379
- 1380 **Sporacestra pertexta** (Nyl.) Stapnes & Timdal, **comb. nov.** [MB 824510] ≡ *Lecidea pertexta* Nyl., in  
1381 Triana & Planchon, Ann. Sci. Nat., Bot., Ser. 4, 19: 347. 1863. ≡ *Phyllopsora pertexta* (Nyl.)  
1382 Swinscow & Krog, Lichenologist 13: 244. 1981. – Holotype: Cuba. "in ins. Cuba", C. Wright (H-  
1383 NYL 17344, left and right hand specimens!).  
1384
- 1385 **Stirtoniella** D.J. Galloway, Hafellner & Elix\*\*, Lichenologist 37: 262. 2005. – Type: *Stirtoniella kelica*  
1386 (Stirt.) D.J. Galloway, Hafellner & Elix (holotype) [= *Lecidea kelica* Stirt.].  
1387

- 1388 ***Thalloidima*** A. Massal.\*\*, Ric. Auton. Lich. Crost.: 95. 1852. – Type: *Thalloidima candidum* (Weber) A.  
1389 Massal. (lectotype designated by Clements & Shear 1931: 319) [= *Toninia candida* (Weber) Th.  
1390 Fr.; = *Lichen candidus* Weber].  
1391 = *Skolekites* Norman\*\*, Conat. Praem. Gen. Lich.: 23. 1852. – Type: *Skolekites candidus* (Weber)  
1392 Norman (lectotype designated by Hafellner 1984: 264) [= *Thalloidima candidum* (Weber) A. Massal.; =  
1393 *Toninia candida* (Weber) Th. Fr.; = *Lichen candidus* Weber].  
1394 = *Diphloeis* Clem.\*\*, Gen. Fung.: 76. 1909. – Type: *Diphloeis candida* (Weber) Clem. (holotype)  
1395 [= *Thalloidima candidum* (Weber) A. Massal.; = *Toninia candida* (Weber) Th. Fr.; = *Lichen candidus*  
1396 Weber].  
1397 = *Thalloedematomyces* Cif. & Tomas.\*\*, Atti Ist. Bot. Lab. Crittog. Univ. Pavia 10: 39, 66. 1953;  
1398 nom. illeg. (Art. 52.1, superfluous name for *Thalloidima*). – Type: *Thalloedematomyces candidi* Cif. &  
1399 Tomas., nom. illeg. (holotype) [= *Thalloidima candidum* (Weber) A. Massal.; = *Toninia candida* (Weber)  
1400 Th. Fr.; = *Lichen candidus* Weber].  
1401 = *Bacillina* Nyl.\*\*, Lich. Env. Paris: 7. 1896. – Type: *Bacillina antipolitana* Nyl. (holotype)  
1402 [= *Thalloidima physaroides* (Opiz) Kistenich, Timdal, Bendiksby & S. Ekman].  
1403 *Notes.* – This genus was included in *Toninia* by Timdal (1992) and corresponds to his species  
1404 groups 1 (with the exclusion of four species now placed in *Kiliasia*) and 10. Morphologically, the genus  
1405 is characterized by the presence of a grey, K+ violet, N+ violet pigment (‘Thalloidima-grün’ or  
1406 ‘Sedifolia-grey’, Meyer & Printzen 2000) in the epitecium and rim of the exciple, with the exception of  
1407 *T. toninianum* (from group 10) which has an olivaceous brown to green, K-, N+ violet pigment. The  
1408 thallus is mostly flattened squamulose to bullate, but two species are non-lichenized. Most species,  
1409 perhaps all, are parasitic on cyanolichens when young or remain parasitic. The ascospores are mostly  
1410 ellipsoid to fusiform, 1-septate, rarely acicular, 3-septate.  
1411 According to our molecular phylogeny (Figs. 2, S2), the following species belong in the genus:  
1412 *Thalloidima albilabrum* (Dufour) Flagey [= *Toninia albilabra* (Dufour) H. Olivier], *Thalloidima*  
1413 *alutaceum* Anzi [= *Toninia alutacea* (Anzi) Jatta], *Thalloidima candidum* (Weber) A. Massal. [= *Toninia*  
1414 *candida* (Weber) Th. Fr.], *Thalloidima diffractum* (A. Massal.) A. Massal. [= *Toninia diffracta* (A.  
1415 Massal.) Zahlbr.], *Thalloidima massatum* (Tuck.) Kistenich, Timdal, Bendiksby & S. Ekman,  
1416 *Thalloidima opuntioides* (Vill.) Kistenich, Timdal, Bendiksby & S. Ekman, *Thalloidima physaroides*  
1417 (Opiz) Kistenich, Timdal, Bendiksby & S. Ekman, *Thalloidima rosulatum* Anzi [= *Toninia rosulata*  
1418 (Anzi) H. Olivier], *Thalloidima sedifolium* (Scop.) Kistenich, Timdal, Bendiksby & S. Ekman,  
1419 *Thalloidima tauricum* Szatala [= *Toninia taurica* (Szatala) Oxner], *Thalloidima toepfferi* Stein [= *Toninia*  
1420 *toepfferi* (Stein) Návas], and *Thalloidima toninianum* (A. Massal.) A. Massal. [= *Toninia toniniana* (A.  
1421 Massal.) Zahlbr.].  
1422 The following species are included here in *Thalloidima* because of morphological similarities with  
1423 one or more of the species listed above even though DNA sequences are not available: *Thalloidima*  
1424 *arcticum* (Timdal) Timdal, *Thalloidima collematicola* (Timdal) Timdal, *Thalloidima ioessum* (Herre) S.  
1425 Ekman & Timdal, *Thalloidima leptogii* (Timdal) Timdal, and *Thalloidima subdiffractum* (Timdal)  
1426 Timdal.  
1427  
1428 ***Thalloidima arcticum*** (Timdal) Timdal, **comb. nov.** [MB 824416] = *Toninia arctica* Timdal, Opera Bot.  
1429 110: 37. 1992. – Holotype: Canada. Northwest Territories, Inuvik, Banks Island, 73°13'N,  
1430 119°32'W, alt. 50–55 m, *Dryas-Oxytropis* and *Carex* community types, 1979, G.W. Scotter 30146  
1431 (CANL!).  
1432  
1433 ***Thalloidima collematicola*** (Timdal) Timdal, **comb. nov.** [MB 824417] = *Toninia collematicola* Timdal,  
1434 Opera Bot. 110: 57. 1992. – Holotype: Italy. Lombardia, Sondrio, along the road from Bormio to  
1435 Bormio 2000, above the village S. Pietro, 46°27'N, 10°23'E, alt. 1530 m, on *Collema* on limestone,  
1436 1988, J. Holtan-Hartwig & E. Timdal 6724 (O L-119!).  
1437  
1438 ***Thalloidima ioessum*** (Herre) S. Ekman & Timdal, **comb. nov.** [MB 824496] = *Bacidia ioessa* Herre,  
1439 Proc. Wash. Acad. Sci. 12: 98. 1910. – Type: USA. California, Santa Clara Co., “on igneous rock  
1440 on a dry hill side, Hidden Villa Cañon, at an altitude of 800 feet”, no later than 1908, A. W. C. T.  
1441 Herre (original material expected to be deposited in UC or FH could not be located). **Neotype**  
1442 **(designated here)**: USA. California, Santa Clara Co., just SW of Los Altos Hills, on the S-facing  
1443 slope of the hills on the E side of the canyon stretching from Moody Rd to Hidden Villa, 2008, S.  
1444 Ekman 3690 (UPS L-878230!).

- 1445 = *Toninia submexicana* B. de Lesd., Lich. Mexique: 25. 1914. – **Lectotype (designated here):**  
 1446 Mexico. Michoacan, Morelia, lomas à l'ouest du Zapote, 1910, A.G. Brouard (O L-829!).  
 1447
- 1448 ***Thalloidima leptogii*** (Timdal) Timdal, **comb. nov.** [MB 824418] ≡ *Toninia leptogii* Timdal, Opera Bot.  
 1449 110: 68. 1992. – Holotype: Italy. Calabria, Cosenza, Valle del Caronte, Ponte Alimena (= ca. 800  
 1450 m E of Mendicino), 39°16'N, 16°13'E, alt. 450 m, 1988, J.C. Hughes & E. Timdal 6803 (O L-  
 1451 121!).  
 1452
- 1453 ***Thalloidima massatum*** (Tuck.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824413] ≡  
 1454 *Lecidea massata* Tuck, Lich. Calif.: 25. 1866. ≡ *Toninia massata* (Tuck.) Herre, Proc. Wash.  
 1455 Acad. Sci. 12, 2: 103. 1910 – Holotype: USA. California, San Fransisco, loose gravelly soil on the  
 1456 west side of last hills near the ocean, H.N. Bolander 75 (FH-TUCK!).  
 1457
- 1458 ***Thalloidima opuntiooides*** (Vill.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824414] ≡  
 1459 *Lichen opuntiooides* Vill., Hist. Pl. Dauphiné 3: 967, Tab. 55. 1789. ≡ *Toninia opuntiooides* (Vill.)  
 1460 Timdal, Opera Bot. 110: 76. 1992. – Neotype (designated by Timdal 1992: 76): France. Alpes-du-  
 1461 Haute-Provence, Gorges du Bachelard, 3.1 km along the road S of Uvernet-Fours, 44°20'N,  
 1462 6°38'E, alt. 1300 m, 1989, E. Timdal 7261 (O L-122!).  
 1463
- 1464 ***Thalloidima physaroides*** (Opiz) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824493] ≡  
 1465 *Lecidea physaroides* Opiz, Lotos 6: 158. 1856. ≡ *Toninia physaroides* (Opiz) Zahlbr., Cat. Lich.  
 1466 Univ. 4: 275. 1926. – Holotype: Czech Republic. Středočeský, Prosik, 1854, F.M. Opiz (PRM  
 1467 698368!).  
 1468
- 1469 ***Thalloidima sedifolium*** (Scop.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824415] ≡  
 1470 *Lichen sedifolius* Scop., Fl. Carniol., Ed. 2, 2: 395. 1772. ≡ *Toninia sedifolia* (Scop.) Timdal,  
 1471 Opera Bot. 110: 93. 1992. – Neotype (designated by Timdal 1992: 93): Italy. Friuli-Venezia-  
 1472 Giulia, Trieste, Monrupino, 45°42'N, 13°48'E, alt. 320 m, in soil-filled crevices in calcareous rock,  
 1473 1988, J.C. Hughes & E. Timdal 6808 (O L-123!).  
 1474
- 1475 ***Thalloidima subdiffractum*** (Timdal) Timdal, **comb. nov.** [MB 824421] ≡ *Toninia subdiffracta* Timdal,  
 1476 Opera Bot. 110: 100. 1992. – Holotype: USA. Utah, Grand Co., Colorado River at Dewey bridge,  
 1477 38°48'N, 109°19'W, alt. 2130 m, on steep rock wall, facing north, 1988, E. Timdal 6890 (O L-  
 1478 124!).  
 1479
- 1480 ***Thamnolecania*** (Vain.) Gyeln.\*\*, Acta Fauna Fl. Universali, Ser. 2, Bot. 1, 5–6: 8. 1933. ≡ *Lecanora*  
 1481 subgen. *Thamnolecania* Vain., Résult. Voy. Belgica, Lich.: 16. 1903. – Type: *Thamnolecania*  
 1482 *brialmontii* (Vain.) Gyeln. (lectotype designated by Dodge 1948: 181) [≡ *Lecanora brialmontii*  
 1483 Vain.].  
 1484
- 1485 ***Tibellia*** Vězda & Hafellner<sup>o</sup> in Hafellner & Vězda, Nova Hedwigia 55: 186. 1992. – Type: *Tibellia*  
 1486 *dimerelloides* Vězda & Hafellner (holotype).  
 1487
- 1488 ***Toninia*** A. Massal.\*\*, Ric. Auton. Lich. Crost.: 107. 1852, nom. cons. – Type: *Toninia cinereovirens*  
 1489 (Schaer.) A. Massal. (lectotype designated by Baumgärtner 1979: 30) [≡ *Lecidea cinereovirens*  
 1490 Schaer.].  
 1491 ≡ *Syncomista* Nieuwl.\*\*, Amer. Midl. Naturalist 4: 386. 1916, nom. nov. pro *Toninia* A. Massal.,  
 1492 nom. illeg. (Art. 52.1). – Type: the type of *Toninia*.  
 1493 = *Arthrosporium* A. Massal.\*\*, Mem. Lichenogr.: 127. 1853. – Type: *Arthrosporium populorum* A.  
 1494 Massal., Mem. Lichenogr.: 128 (1853) (holotype) [≡ *Toninia populorum* (A. Massal.) Kistenich,  
 1495 Timdal, Bendiksby & S. Ekman].  
 1496 ?= *Leptographa* Jatta<sup>o</sup>, Bull. Soc. Bot. Ital. 1: 211. 1892. – Type: *Leptographa toninioides* Jatta  
 1497 (holotype).  
 1498 *Notes.* – The genus was monographed by Timdal (1992). It is split here into five genera based on  
 1499 our molecular phylogeny (Figs. 2, S2): *Bibbya*, *Kiliasia*, *Thalloidima*, *Toninia*, and *Toniniopsis*. In the  
 1500 new circumscription, *Toninia* corresponds to the species groups 2, 6, 9 and partly 5 and 7 of Timdal  
 1501 (1992), with the inclusion of the genus *Arthrosporium* and some species of *Bacidia*. *Toninia* species have  
 1502 a green, K–, N+ violet ('Bacidia-grün' or 'Bagliettoana-green', Meyer & Printzen 2000) or brown, K–,

1503 N– pigment in the epithecium and exciple; ellipsoid to acicular, (0-) 1- pluriseptate ascospores; and either  
1504 non-lichenized or a thallus varying from flattened squamulose to bullate.

1505 According to our molecular phylogeny (Figs. 2, S2), the following species belong in the genus:  
1506 *Toninia cinereovirens* (Schaer.) A. Massal., *Toninia plumbina* (Anzi) Hafellner & Timdal, *Toninia*  
1507 *populorum* (A. Massal.) Kistenich, Timdal, Bendiksby & S. Ekman, *Toninia squalida* (Ach.) A. Massal.,  
1508 *Toninia subdispersa* (Nyl.) K. Knudsen and *Toninia tristis* (Th. Fr.) Th. Fr.

1509 In addition, the following species are currently included in the *Toninia*, but the lack of DNA  
1510 sequences and diagnostic morphological characters makes this position uncertain: *T. corallina* Timdal, *T.*  
1511 *gobica* N.S. Golubk., *T. himalayana* Timdal, *T. nashii* Timdal, *T. poeltiana* S.Y. Kondr., Lökös & Hur, *T.*  
1512 *poeltii* Timdal, *T. subfuscae* (Arnold) Timdal, *T. subtalparum* van den Boom, *T. ualae* Etayo, *T.*  
1513 *verrucariae* (Nyl.) Timdal, and *T. wetmorei* Timdal.

1514

1515 ***Toninia populorum*** (A. Massal.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824425] ≡  
1516 *Arthrosporium populorum* A. Massal., Mem. Lichenogr.: 128. 1853. – Holotype: Italy, “Garda ad  
1517 populos”, A. Massalongo (VER!).

1518

1519 ***Toniniopsis*** Frey\*\*, Ber. Schweiz. Bot. Ges. 35: 73. 1926. – Type: *Toniniopsis obscura* Frey (holotype)  
1520 [= *Toniniopsis illudens* (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman].

1521 *Notes.* – This genus consists of species previously placed in *Bacidia* and *Toninia*, and the  
1522 separation of the two genera in this species complex was discussed by Timdal (1992: 23) and Ekman  
1523 (1996a: 44). We unite these these species in the previously described genus *Toniniopsis*. This genus is  
1524 morphologically similar to *Toninia* but differs in the generally stronger pigmentation of the exciple. The  
1525 green pigment occurring in the epithecium in most species is believed to be same as in *Toninia* (‘*Bacidia*-  
1526 grün’ or ‘Bagliettoana-green’, Meyer & Printzen 2000).

1527 According to our molecular phylogeny (Figs. 2, S2), the following species belong in the genus:  
1528 *Toniniopsis aromatica* (Sm.) Kistenich, Timdal, Bendiksby & S. Ekman, *T. coelestina* (Anzi) Kistenich,  
1529 Timdal, Bendiksby & S. Ekman, *T. subincompta* (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman, *T.*  
1530 *verrucarioides* (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman, and the species currently known as  
1531 *Bacidia bagliettoana* (A. Massal. & De Not.) Jatta. The complicated nomenclature of this latter species  
1532 makes us refrain from making any new combination at the moment.

1533 The following species are included here in *Toniniopsis* because of morphological similarities with  
1534 one or more of the species listed above, even though DNA sequences are not available: *T. cretica*  
1535 (Timdal) Timdal, and *T. mesoidea* (Nyl.) Timdal.

1536

1537 ***Toniniopsis aromatica*** (Sm.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824495] ≡  
1538 *Lichen aromaticus* Sm. in Smith & Sowerby, Engl. Bot. 25, Tab. 1777. 1807 ≡ *Toninia aromatica*  
1539 (Sm.) A. Massal., Framm. Lichenogr.: 24. 1855. – Lectotype (designated by Baumgärtner 1979:  
1540 114): UK. England, Norfolk, near Yarmouth, *D. Turner* (BM!).

1541

1542 ***Toniniopsis coelestina*** (Anzi) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824430] ≡  
1543 *Bacidia coelestina* Anzi, Atti Soc. Ital. Sci. Nat. 9: 251. 1866. ≡ *Toninia coelestina* (Anzi) Vězda,  
1544 Cas. Slez. Mus., Ser. A, Hist. Nat. 10: 105. 1961. – Lectotype (designated by Timdal 1992: 56):  
1545 Italy. Lombardia, Sondrio, in rimulis rupium calcarearum, septentrionem spectantium, in valle di  
1546 Fraéle, alt. 1900–2200 m, *s. coll.* [Anzi, Lich. Rar. Langob. 517] (UPS!).

1547

1548 ***Toniniopsis cretica*** (Timdal) Timdal, **comb. nov.** [MB 824434] ≡ *Toninia cretica* Timdal, Opera Bot.  
1549 110: 59. 1992. – Holotype: Greece. Crete, Khandia, at the top of the gorge from Komitades to  
1550 Imbros, 35°15'N, 24°15'E, alt. 740 m, in fissures in calcareous rock, 1988, *E. Timdal* 6692 (O L-  
1551 120!).

1552

1553 ***Toniniopsis illudens*** (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824426] ≡  
1554 *Lecidea illudens* Nyl., Flora 53: 34. 1870. – Lectotype (**designated here**): Finland. Kuusamo,  
1555 Kitkajoki, 19 Aug 1867, *F. Silén* (H-NYL 17322!); isolectotype (UPS L-513287!).  
1556 = *Toniniopsis obscura* Frey, Ber. Schweiz. Bot. Ges. 35: 73. 1926. – Lectotype (designated by  
1557 Ekman 1996: 130): Switzerland. Val Cluozza, auf Kalkfelsgesimsen im Pinetum mont., alt. 1850 m,  
1558 1923, *E. Frey* 442 (BERN!).

1559

- 1560 ***Toniniopsis mesoidea*** (Nyl.) Timdal, **comb. nov.** [MB824436] ≡ *Lecidea mesoidea* Nyl., Flora 51: 475.  
 1561 1868. ≡ *Toninia mesoidea* (Nyl.) Zahlbr., Cat. Lich. Univ. 4: 289. 1926. – Holotype: UK. Channel  
 1562 Islands, ‘Ins. Sark’, 1868, *C. Larbalestier* (H-NYL 16719!).  
 1563
- 1564 ***Toniniopsis subincompta*** (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB824431] ≡  
 1565 *Lecidea subincompta* Nyl., Flora 48: 147. 1865. ≡ *Bacidia subincompta* (Nyl.) Arnold, Flora 53:  
 1566 472. 1870. – Type to be proposed for conservation: Austria. An Stämmchen von *Sorbus*  
 1567 *chamaespilus* unterhalb der Serloswände ober der Waldrast, Matrei in Tirol, alt. 5400 ft, 1872,  
 1568 *F. Arnold* [Arnold, Lich. Exs. No 505] (H-NYL 17400!).  
 1569
- 1570 ***Toniniopsis verrucarioides*** (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman, **comb. nov.** [MB 824433]  
 1571 ≡ *Lecidea aromatica* var. *verrucarioides* Nyl., Bot. Not. 1853: 157. 1853. ≡ *Lecidea*  
 1572 *verrucarioides* (Nyl.) Nyl., Actes Soc. Linn. Bordeaux 21: 369. 1856. ≡ *Toninia verrucarioides*  
 1573 (Nyl.) Timdal, Opera Bot. 110: 116. 1992. – Lectotype (designated by Timdal 1992: 116): France.  
 1574 Hautes-Pyrénées, Bagnières de Bigorre, *W. Nylander* (H-NYL 16804!).  
 1575
- 1576 ***Tylohallia*** P. James & H. Kiliass\*\* in Kiliass, Herzogia 5: 409. 1981. – Type: *Tylohallia biformigera*  
 1577 (Leight.) P. James & H. Kiliass (holotype) [≡ *Lecidea biformigera* Leight.].  
 1578
- 1579 ***Waynea*** Moberg\*\*, Lichenologist 22: 249. 1990. – Type: *Waynea californica* Moberg (holotype).  
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## AUTHOR CONTRIBUTIONS

All authors participated in the design of the research. MB, SE and SK generated sequences in the lab. SE and SK designed and performed the data analysis. All authors participated actively in the interpretation and discussion of the results. SK wrote the first draft of the manuscript and ET wrote the Taxonomy chapter. All authors corrected and improved the manuscript.

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1894 **Table S1.** Median character state probabilities under three different priors for the Ramalinaceae MRCA  
1895 and five selected subclades (Fig. 2: clade C–G) that we have named the *Bacidia*-, *Toninia*-, *Rolfidium*-,  
1896 *Biatora*-, and *Ramalina*-group, respectively. The three tested priors: equal, Yang, and maddfitz (=   
1897 Maddision & FitzJohn).  
1898  
1899



1900 **Fig. 1.** Photograph of *Phyllopsora breviscula* (type species) illustrating the phyllopsoroid growth  
1901 form with the areoles/squamules overgrowing a thick prothallus (B 60 0083819); scale bar = 2 mm.  
1902

1903 **Fig. 2.** Extended majority rule consensus tree resulting from the Bayesian MCMC analysis of the  
1904 5-locus alignment with Bayesian PP  $\geq 0.7$  and/or Garli maximum likelihood BS  $\geq 50$  and branch lengths.  
1905 Strongly supported branches (PP  $\geq 0.95$  and BS  $\geq 75$ ) are marked in bold; strongly supported branches  
1906 with BS  $\geq 95$  are also marked with a dot above the branch; branches with PP  $\geq 0.95$  and BS  $< 70$  are  
1907 marked in bold grey; branches only supported with PP  $\geq 0.7$  or BS  $\geq 50$  are marked with an asterisk  
1908 above the branch. The starting node of the Ramalinaceae is indicated with an arrow, PP (above branch)  
1909 and BS (below branch). Family affiliations according to Lücking & al. (2017a, b). *Boreoplaca*  
1910 *ultrafrigida* and *Ropalospora lugubris* were used for rooting. Seven major clades are distinguished (A–  
1911 G). Terminals are named according to the taxonomy prior to this study. Our revised genus affiliation is  
1912 indicated to the right. The character state matrix for the coded taxa is provided to the far right.  
1913 Abbreviations used: SL = spore length, SS = spore septation, GF = growth form, CZ = climate zone, CH  
1914 = climate humidity, SU = substrate, VD = vegetative dispersal; U = unknown. See Material & Methods  
1915 for coding specifics.  
1916

1917 **Fig. 3.** Photographs of the newly described genera. **a** *Bellicidia incompta* (O-L-175984), **b**  
1918 *Parallopsora leucophyllina* (O-L-144645); scale bar = 1 mm.  
1919

1920 **Fig. S1.** Extended majority rule consensus tree resulting from the Bayesian MCMC analysis on the  
1921 2-locus alignment with Bayesian PP  $\geq 0.7$  and/or Garli maximum likelihood BS  $\geq 50$  and branch lengths.  
1922 Strongly supported branches (PP  $\geq 0.95$  and BS  $\geq 75$ ) are marked in bold; strongly supported branches  
1923 with BS  $\geq 95$  are also marked with a dot above the branch; branches with PP  $\geq 0.95$  and BS  $< 70$  are  
1924 marked in bold grey; branches only supported with PP  $\geq 0.7$  or BS  $\geq 50$  are marked with an asterisk  
1925 above the branch. The starting node of the Ramalinaceae is indicated with an arrow, PP (above branch)  
1926 and BS (below branch). Family affiliations according to Lücking & al. (2017a, b). *Boreoplaca*  
1927 *ultrafrigida* and *Ropalospora lugubris* were used for rooting. Seven major clades are distinguished (A–  
1928 G). Terminals are named according to the taxonomy prior to this study. The revised genus affiliation is  
1929 indicated on the right.  
1930

1931 **Fig. S2.** Phylogenetic hypothesis of *Toninia* species and presumed close relatives based on all  
1932 available ITS sequences. The DNA sequences with GenBank Accession Numbers MG838156 –  
1933 MG838203 were produced at the Canadian Centre for DNA Barcoding (CCDB; www.ccdb.ca) for the  
1934 OLICH project (nhm2.uio.no/olich) at the Norwegian Barcode of Life project (NorBOL;  
1935 www.norbol.org). The sequences for the remaining accessions were produced as described in the Material  
1936 and methods section. The phylogenetic analysis followed the description for the 5-locus and 2-locus  
1937 alignment. *Bacidia rosella* was used for rooting. The figure shows the extended majority rule consensus  
1938 tree resulting from the Bayesian MCMC analysis with Bayesian PP  $\geq 0.95$  (above branch) and Garli  
1939 maximum likelihood BS  $\geq 70$  (below branch) and branch lengths. GenBank accession and BOLD record  
1940 (starting with BARLI) numbers are included in the respective terminal descriptions. Our revised genus-  
1941 level taxonomy is indicated on the right.





*Ropalospora lugubris* (Ropalosporaceae)

*Boreoplaca ultrafrigida* (Ophioparmaceae)

*Catolechia wahlenbergii* (Rhizocarpaceae)

*Physcia aipolia* (Physciaceae)

*Catlinaria atropurpurea* (Ramalinaceae)

*Speerschnneidera euploca* (Leprocaulaceae)

*Teloschistes flavicans* (Teloschistaceae)

*Porpidinia tumidula* I (Lecideaceae)

*Porpidinia tumidula* II (Lecideaceae)

*Phyllopsora lividocarpa* (Ramalinaceae)

*Phyllopsora atrocarpa* (Ramalinaceae)

*Phyllopsora nigrocincta* (Ramalinaceae)

*Toninia thiopora* (Ramalinaceae)

*Psoroma karstenii* II (Pannariaceae)

*Herteliana taylorii* (Squamarinaceae)

*Squamarina gypsacea* (Squamarinaceae)

*Psorinia conglomerata* (Lecanoraceae)

*Frutidella caesioides* (Ramalinaceae)

*Adolecacia pilati* (Ramalinaceae)

*Lecanora poliophaea* (Lecanoraceae)

*Tasmidella variabilis* (Ramalinaceae)

*Japewia tornuensis* I (Ramalinaceae)

*Japewia tornuensis* II (Ramalinaceae)

*Austrolecia antarctica* (Catillariaceae)

*Tephromela atra* (Tephromelataceae)

*Catillaria erysiboides* I (Catillariaceae)

*Catillaria erysiboides* II (Catillariaceae)

*Catillaria contristans* I (Catillariaceae)

*Catillaria contristans* II (Catillariaceae)

*Schadonia fecunda* (Ramalinaceae)

*Glyphopeltis ligustica* (Psoraceae)

*Psora decipiens* (Psoraceae)

*Protoblastenia rupestris* (Psoraceae)

*Physcidia* sp.

*Phyllopsora borbonica*

*Phyllopsora pertexta*

*Phyllopsora sorediata*

*Physcidia cylindrophora* II

*Bacidia wellingtonii*

*Bacidia arceutina*

*Bacidia absistens*

*Bacidiodorsia squamulosula*

*Bacidia rosella*

*Bacidia schweinitzii*

*Lueckingia polyspora*

*Toninia candida* I

*Toninia candida* II

*Toninia physaroides* I

*Toninia physaroides* II

*Toninia toniniana* I

*Toninia toniniana* II

*Toninia bullata* I

*Toninia bullata* II

*Toninia auriculata*

*Bacidia vermicera*

*Toninia sculpturata* I

*Toninia sculpturata* II

*Toninia athallina*

*Toninia aromatica*

*Toniniopsis obscura*

*Bacidia subincompta*

*Toninia coelestina*

*Bacidia bagliettoana*

*Toninia cinereo-virens*

*Toninia squalida*

*Toninia tristis*

*Arthrosporium populorum*

*Waynea californica*

*Aciculopsora salmonae*

*Bacidia circumspecta*

*Bacidia auerswaldii*

*Phyllopsora labriformis*

*Phyllopsora brakoae*

*Phyllopsora leucophyllina*

*Eschatogonia prolifera* I

*Eschatogonia prolifera* II

——— PP ≥ 0.95 and BS ≥ 75  
 ● PP ≥ 0.95 and BS ≥ 95  
 ——— PP ≥ 0.95 and BS < 75  
 ★ PP ≥ 0.7 or BS ≥ 50

	SL	SS	GF	CZ	CH	SU	VD
U	U	3	2	1	2	1	1
1	0	3	2	1	2	0	0
1	0	3	2	1	2	0	0
1	0	3	2	1	2	1	1
1	0	3	2	1	2	1	1
1	2	0	1	1	2	0	0
1	2	0	1	1	2	0	0
1	2	0	1	1	2	0	0
1	2	3	2	1	2	1	1
1	2	0	1	1	2	0	0
1	2	0	1	1	2	0	0
0	0	0	2	1	2	0	0
1	1	0	1	0	1	0	0

**Sporacestra**

**Bacidia**

**Lueckingia**

**Thalloidima**

**Bibbya**

**Killasia**

**Toniniopsis**

**Toninia**

**Waynea**

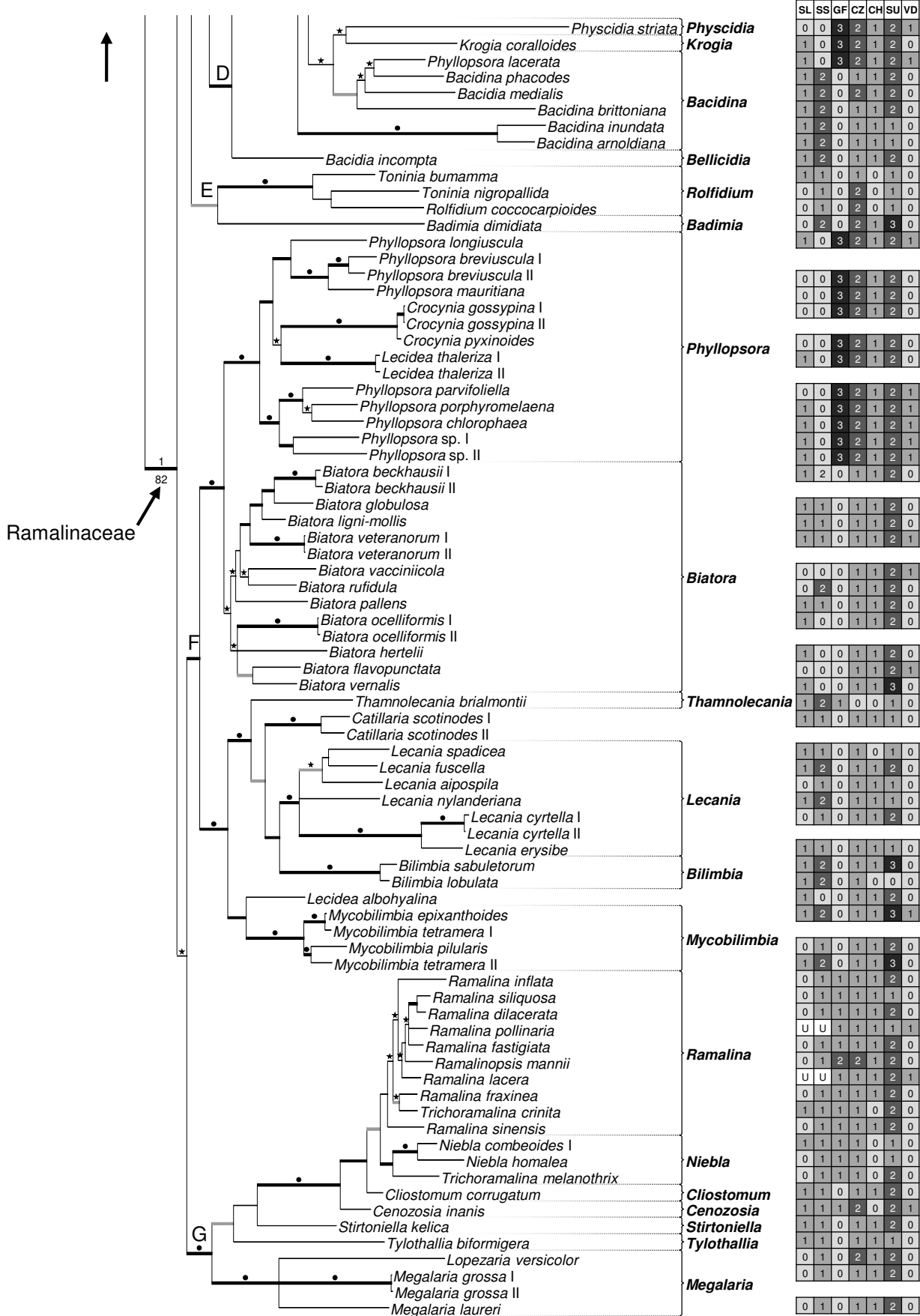
**Aciculopsora**

**Scutula**

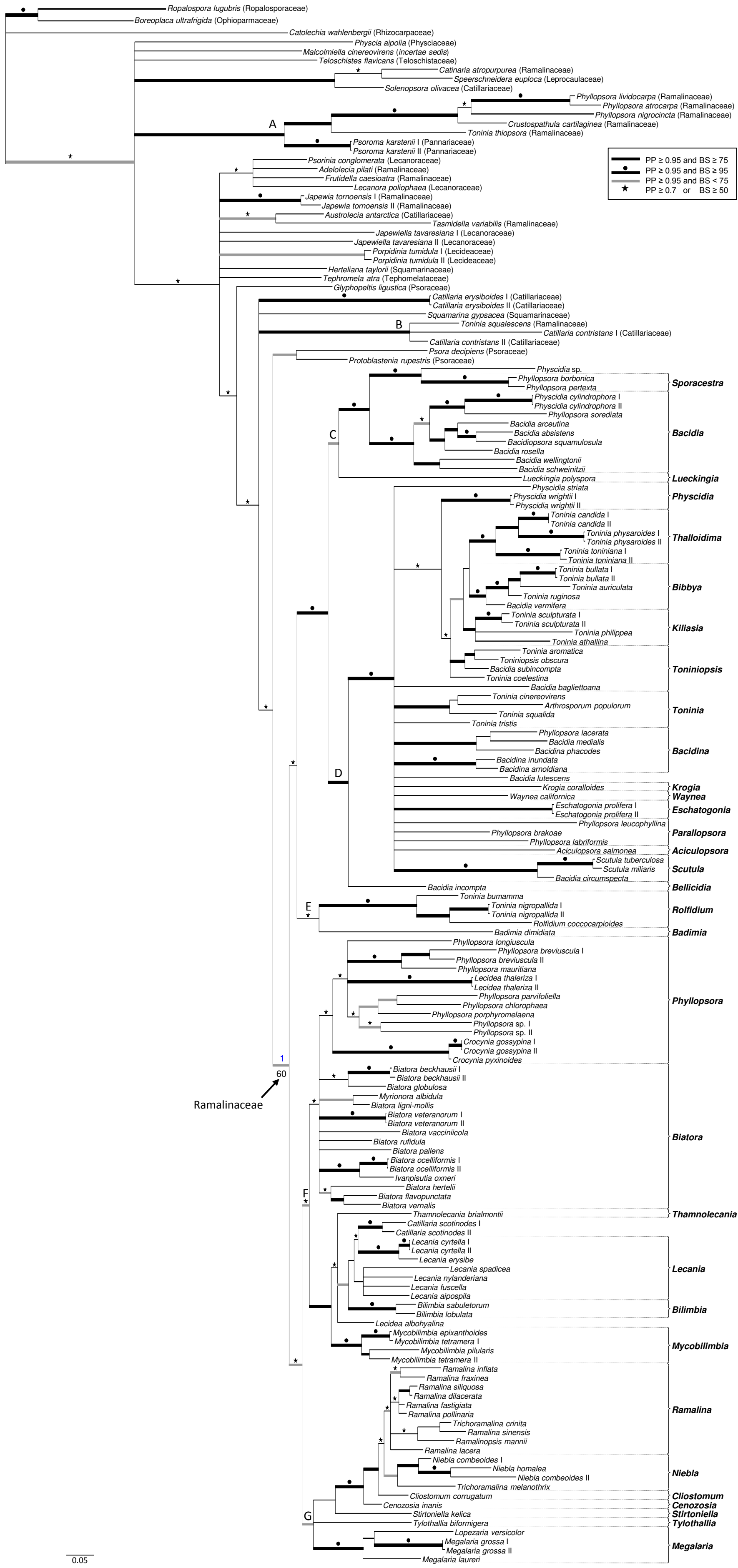
**Parallopsora**

**Eschatogonia**









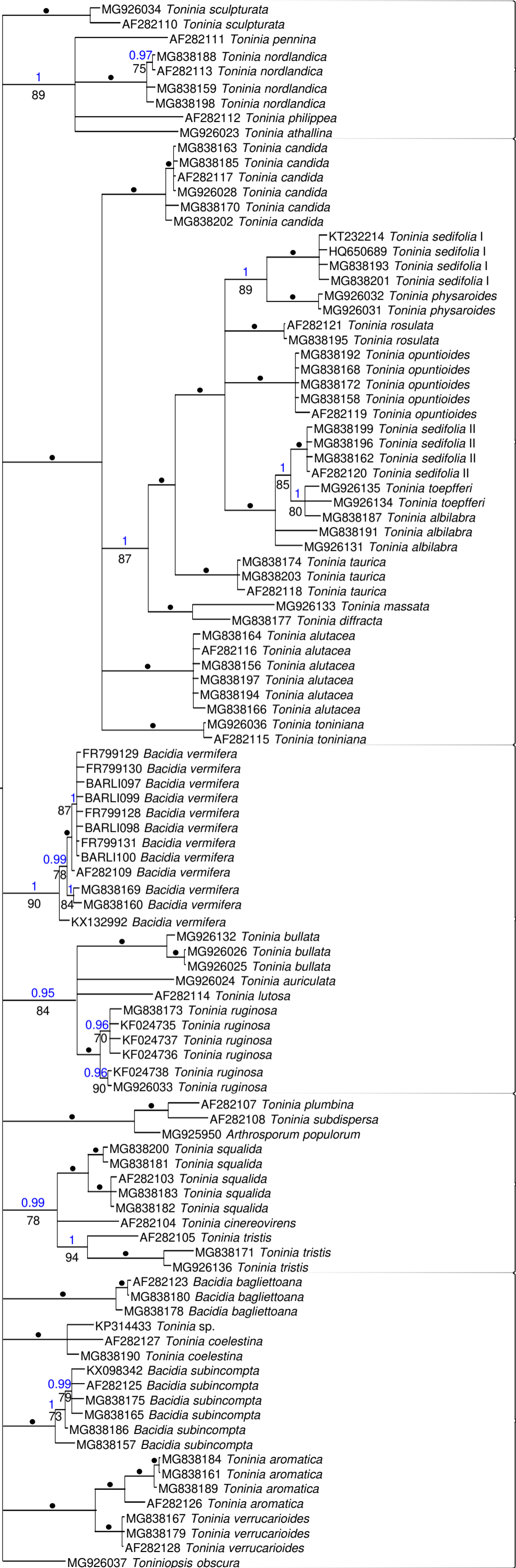
● PP ≥ 0.95 and BS ≥ 75  
 — PP ≥ 0.95 and BS ≥ 95  
 — PP ≥ 0.95 and BS < 75  
 ★ PP ≥ 0.7 or BS ≥ 50

Ramalinaceae

1

60

AF282086 *Bacidia rosella*



**Kiliasia**

**Thalloidima**

**Bibbya**

**Toninia**

**Toniniopsis**