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Reclassification of species in the lichenized family Gomphillaceae Walt. Watson ex Hafellner (Ascomycota: Graphidales) using morphology-based phylogenetic binning

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ABSTRACT
Results of phylogenetic analyses are often not translated into formal classifications, because only a portion of the taxa have been sequenced, making the placement of the remaining taxa unclear. This is the case for Gomphillaceae Walt. Watson ex Hafellner, which currently includes 422 accepted lichenized and 18 lichenicolous or fungicolous species, with only 27% having sequence data available. A separate, expanded phylogeny of the family recognized at least 19 further genus-level lineages, in addition to the 27 genera thus far distinguished, for a total of 46, making it necessary to reassess generic placement of a large number of non-sequenced species and to test the stability of the newly proposed classification. In the present study we applied the phenotype-based phylogenetic binning approach to address this problem. We selected 310 taxa, leaving out most species of *Gyalidea* Lettau ex Vězda and part of *Gyalideopsis* Vězda and *Gyalectidium* Müll. Arg., because the phylogenetic framework was either not yet well established (*Gyalidea*, *Gyalideopsis*) or the genus was well-defined phenotypically (*Gyalectidium*). Of the 310 selected species, 72 had sequence data available and served as reference taxa. The binning analysis for the 238 remaining taxa for which no molecular data were available placed 157 taxa (66%) with absolute support (100%) into a single node in the reference tree. Further 35 taxa appeared on two or more alternative nodes but had at least 90% support for one of these nodes. Another 24 taxa had between 70% and 89% support for a given node, resulting in a total of 216 out of 238 taxa (91%) with a supported placement in the tree. Of these, 181 were placed within one of the 46 genus-level lineages, whereas 35 clustered with unnamed nodes, indicating further, potentially

unrecognized genera. These mostly included non-foliicolous species of *Gyalideopsis* and relatives for which no sequenced taxa were in the molecular reference tree. Three further species of *Gyalideopsis* were placed with the outgroup. Most of the placements obtained through phylogenetic binning were consistent with anticipated placements from earlier studies. Only for a small portion of the taxa (about 10%), the binning results were in conflict with their current or previously predicted placement.

KEY WORDS
Foliicolous lichens, phenotype data, molecular data, phylogenetic binning, maximum likelihood.

RÉSUMÉ
Reclassification des lichens de la famille Gomphillaceae Walt. Watson ex Hafellner (Ascomycota : Graphidales) à l'aide du regroupement phylogénétique basé sur la morphologie.
Les résultats de l'analyse phylogénétique ne sont souvent pas traduits en classifications formelles, car seule une partie des taxons a été séquencée, ce qui rend le placement des taxons restants peu clair. C'est le cas pour les Gomphillaceae Walt. Watson ex Hafellner, qui comprennent actuellement 422 espèces lichénisées et 18 espèces lichénicoles ou fongicoles acceptées, avec seulement 27% ayant des données de séquence disponibles. Une mise à jour de la phylogénie chez cette famille a permis la reconnaissance d'au moins 19 lignées supplémentaires ou nouvelles au niveau du genre, en plus des 27 genres connus jusqu'à présent, ce qui a rendu nécessaire de réévaluer le placement générique de nombreuses espèces non séquencées et de tester la stabilité des nouvelles lignées résultantes. Dans la présente étude, nous avons donc appliqué l'approche de regroupement phylogénétique à cette famille. Nous avons sélectionné un sous-ensemble de 310 espèces, en laissant de côté la plupart des espèces de *Gyalidea* Lettau ex Vězda et une partie de *Gyalideopsis* Vězda et *Gyalectidium* Müll. Arg., soit parce que le cadre phylogénétique n'était pas encore bien établi pour ces genres (*Gyalidea*, *Gyalideopsis*), soit parce que le genre était par ailleurs bien défini et monophylétique (*Gyalectidium*). Sur les 310 espèces sélectionnées, 72 disposaient de données de séquence et servaient de taxons de référence. L'analyse de regroupement sur les 238 taxons restants et pour lesquels aucune donnée moléculaire n'était disponible a placé 157 taxons (66 %) avec un support absolu (100 %) dans un seul nœud de l'arbre de référence. Trente-cinq autres taxons sont apparus sur deux nœuds alternatifs ou plus, mais avaient au moins 90 % de support pour un nœud ; 24 autres taxons avaient entre 70 % et 89 % de support pour un nœud donné. Ainsi, 216 taxons sur 238 (91 %) avaient un support pour un nœud donné. Cependant, pour 35 d'entre eux, le placement des nœuds se trouvait dans une partie non résolue de l'arbre, indiquant des genres potentiellement non reconnus, comprenant principalement des espèces non foliicoles de *Gyalideopsis* et des taxons apparentés pour lesquels aucune séquence ne se trouvait dans l'arbre de référence. Trois autres espèces de *Gyalideopsis* ont été placées avec l'exogroupe. La plupart des taxons restants pouvaient être placés dans un genre donné en toute confiance, y compris les 19 genres nouvellement reconnus, et la plupart des placements obtenus par regroupement phylogénétique étaient cohérents avec les placements prévus, y compris des études antérieures. Pour une petite partie des taxons seulement (environ 10 %), les résultats du regroupement étaient en conflit avec leur placement actuel ou prédit précédemment.

MOTS CLÉS
Lichens folicoles, données phénotypiques, données moléculaires, binning phylogénétique, plausibilité maximum.

INTRODUCTION

Molecular phylogeny has revolutionized our understanding of relationships between taxa and their classification within the fungi, at all levels from phylum down to species. Since fungi have only a limited set of systematically useful phenotype characters available, molecular data are of particular importance to correctly delimit and classify taxa (James *et al.* 2006; Hibbett *et al.* 2007; McLaughlin *et al.* 2009; Rivas Plata *et al.* 2011, 2012a; Moncada *et al.* 2014; Dal-Forno *et al.* 2016; Spatafora *et al.* 2016; Ahrendt *et al.* 2018; Tedersoo *et al.* 2018; Galindo *et al.* 2021; Wijayawardene *et al.* 2022). Yet, traditionally, the classification of fungi and other organisms has been based on the paradigm that taxa should be recognized on the basis of phenotypic characters. Molecular methods were then used to test and re-investigate the phylogenetic relationships between phenotypically defined lineages (Grube *et al.* 2004; Lutzoni *et al.* 2004; Parnmen *et al.* 2012; Rivas Plata *et al.* 2012b).

Although sequencing methods have become relatively inexpensive and broadly available, often only a fraction of all taxa in a group have molecular data available, usually because fresh material is needed and many species have restricted distributions and/or are rare. Therefore, results of phylogenetic analyses are often not translated into formal classifications, because the placement of non-sequenced taxa remains unclear. Examples are widespread among fungi and a prominent example of tropical lichens is the Graphidaceae, in which about 20% of the known species have been sequenced and, in some genera, such as *Graphis* Adans. and its recent segregate *Allographa* Chevall., only about 10% (Lücking *et al.* 2009; Rivas Plata *et al.* 2011; Lücking & Kalb 2018). Thus, with the profound changes in classification in this family (Rivas Plata *et al.* 2012a; Parnmen *et al.* 2012; Lücking *et al.* 2015), the remaining species have to be placed within a new classification framework based on phenotype data alone.

An approach to overcome this problem is phenotype-based phylogenetic binning, a set of algorithms that provide a quantitative and testable mean to place taxa based on phenotype data within a phylogenetic framework of taxa for which both molecular and phenotype data are available (Berger *et al.* 2011a, b). This method was originally developed to place fossils into a phylogenetic tree but can equally be applied to extant taxa. Phylogenetic binning includes three key components: 1) building a phylogenetic framework (reference tree) using only taxa with molecular data available; 2) mapping phenotype characters onto the phylogeny for these taxa and computing character weights based on their distribution over the tree (homoplastic and uninformative characters are downweighed); and 3) invoking the Evolutionary Placement Algorithm (EPA) for all taxa lacking molecular data. This approach places ('bins') each taxon individually into the tree based on its weighted phenotype characters; it also features bootstrapping to evaluate consistency of the placement (Berger *et al.* 2011a). This method provides predictive, testable taxon placements and can quickly process a large number of taxa, since computational time only increases linearly. Besides providing predictive classifications for taxa lacking molecular data, a specific use of this method consists in the placement of types into a phylogenetic framework in order to fix the name of clades when no molecular data can be obtained from types (Lücking *et al.* 2015). The method can also be used as an identification tool (Lücking *et al.* 2023).

Thus far, phylogenetic binning has been mostly used with lichen fungi, such as Graphidaceae (Berger *et al.* 2011b; Rivas Plata *et al.* 2012b; Parnmen *et al.* 2012; Lücking *et al.* 2015; Lücking & Kalb 2018; Perlmutter *et al.* 2020). The method has also been employed for other organisms, including plants and sponges (Koch *et al.* 2012; Fang *et al.* 2013; Springer *et al.* 2015; Dohrmann *et al.* 2017; Testo *et al.* 2018).

Here, we apply the binning approach to the lichenized family Gomphillaceae, which currently includes 440 accepted species, among them 18 lichenicolous and fungicolous taxa (Lendemer 2017; Lücking *et al.* 2017; Diederich *et al.* 2018; Herrera-Campos *et al.* 2019; Gutteres *et al.* 2020; Roux *et al.* 2022). Lichenized members of this family are mostly found on leaves in wet tropical forests, but several lineages, particularly in the genus *Gyalideopsis s.lat.*, also occur on other substrata and extend into temperate regions (Vězda & Poelt 1987; Kalb & Vězda 1988; Lücking 1997, 2008; Lücking *et al.* 2007; Lendemer 2017). Until recently, only 25 species (6%) had sequence data available, a proportion that was increased to 111 (25%), including several putatively new taxa, through a much expanded taxon sampling (Xavier-Leite *et al.* 2022). This latter study recognized at least 19 new genus-level lineages (Xavier-Leite *et al.* 2022, 2023), in addition to the 27 genera thus far distinguished (Etayo 2017; Lücking *et al.* 2017; Diederich *et al.* 2018; Gutteres *et al.* 2020), making it necessary to reassess generic placement of many additional species, particularly in the highly polyphyletic genera *Aderkomyces* Bat., *Calenia* Müll. Arg., *Echinoplaca* Fée, *Gyalideopsis* Vězda, and *Tricharia* Fée.

MATERIAL AND METHODS

Phenotype data

We relied on the phenotype data matrix first assembled by Lücking *et al.* (2005). This matrix originally contained 209 characters tailored for Gomphillaceae, but was extended here to 223 to allow the inclusion of the taxa previously placed in Asterothyriaceae and Solorinellaceae, namely the genera *Asterothyrium* Müll. Arg., *Gyalidea* Lettau ex Vězda (including *Solorinella* Anzi), *Linhartia* Sacc. & P. Syd., *Phyllogyalidea* Lücking, and *Psorotheciopsis* Rehm (Vězda 1973; Vězda & Poelt 1987; Lücking 1997, 1999, 2008; Aptroot & Lücking 2002; Henssen & Lücking 2002; Lücking *et al.* 2004, 2005). The mentioned genera were recently reclassified in Gomphillaceae (Lücking *et al.* 2017) and were also nested in that family in the most recent phylogenetic analysis (Xavier-Leite *et al.* 2022). In addition, some characters were accommodated to include the outgroup taxon, the genus *Coenogonium* Ehrenb. (Appendix 1).

While the recently published phylogenetic analysis used *Fissurina* Fée (in the sister group Graphidaceae) as outgroup (Xavier-Leite *et al.* 2022), in the binning analysis we opted for *Coenogonium*, an outgroup for both Gomphillaceae and Graphidaceae, which provides a better model for the assessment of ancestral apothecial types in these two families. The 223 characters were divided into five groups: 1) ecology (14 characters); 2) thallus morphology and anatomy (46); 3) apothecial morphology and anatomy (86); 4) hyphophore morphology and anatomy (67 characters); and 5) pycnidial morphology and anatomy (10). The matrix contained a total of 310 ingroup taxa, about 75% of the accepted species of Gomphillaceae, plus three *Coenogonium* outgroup species (Appendix 2). Most species of *Gyalidea* and about one third of the species of *Gyalideopsis* were excluded, since the molecular sampling for these taxa was insufficient to provide reliable binning results. We also included only a part of the genus *Gyalectidium* Müll. Arg., since this genus is phenotypically very distinctive, characterized by unique hyphophores and very uniform apothecial anatomy, and resulted monophyletic in both molecular and cladistic analyses (Ferraro *et al.* 2001; Lücking *et al.* 2004, 2005; Xavier-Leite *et al.* 2022).

Molecular reference tree

For the molecular reference tree, we first ran the same data set as Xavier-Leite *et al.* (2022), based on two molecular markers, the mitochondrial small subunit (mtSSU) and the nuclear large subunit (nuLSU) rDNA (see their supplementary table S1 for GenBank accession numbers), but with three *Coenogonium* species as outgroup (accession numbers AF279387, AF465442, AY300834, AY300884, AY584698, AY584699). We then used a subset of the data, representing one terminal per species, including 72 ingroup species and three outgroup taxa (Appendix 3). To compute the reference tree for the phylogenetic binning, the aligned dataset was subjected to maximum likelihood (ML) tree search using RAxML 8.2.0 (Stamatakis 2006, 2014; Stamatakis *et al.* 2008), employing the universal GTR-gamma model with ten slow

ML searches. To avoid topological artifacts of sampling bias relative to the complete data set, the topology was constrained under RAxML using the topology obtained by Xavier-Leite *et al.* (2022) for the full data set.

Phylogenetic binning

With 75 taxa in the molecular reference tree and 313 in the full phenotype matrix, our goal was to bin 238 taxa based on their phenotype characters into the reference tree. In the first step of the binning method, the molecular reference tree and the matrix of 223 phenotype characters for the 75 sequenced taxa were used to compute a maximum likelihood weight vector in RAxML 7.2.6 (Berger *et al.* 2011a, b) that reflected the distribution of the phenotypic character states over the reference tree. Subsequently, applying the weight vector, the 238 non-sequenced query taxa were placed into the reference tree using the Evolutionary Placement Algorithm (EPA) implemented in RAxML 7.2.6 (Stamatakis *et al.* 2005, 2008; Stamatakis 2006; Berger *et al.* 2011a, b). Potential alternative placements were tested through non-parametric bootstrapping using 100 replicates. The classification tree was visualized in FigTree 1.4.0 (http://tree.bio.ed.ac.uk/software/figtree/); to make output tree file compatible with that program, it needed to be formatted by replacing the string ":1.0[" with "[" and the string "]" with "]:1.0". Also, query name strings with placements having the same bootstrap support and hence representing duplicate names were edited by adding the letters a, b, c, etc., to generate unique name strings for each terminal. The resulting classification table was converted from a space-delimited text into a tab-delimited spreadsheet format to summarize the results.

RESULTS

The molecular reference tree included 35 genus-level lineages, out of the 46 now recognized based on our previous phylogenetic study (Xavier-Leite *et al.* 2022, 2023; Fig. 1). Of these, 19 represented previously recognized and 16 newly recognized genera. The binning analysis for the 238 taxa for which no molecular data were available placed 157 taxa (66%) with absolute support (100%) into a single node in the reference tree (Table 1; Fig. 2; Appendices 4; 5). Further 35 taxa appeared on two or more alternative nodes but had at least 90% support for one of these nodes; another 24 taxa had between 70% and 89% support for a given node. Thus, 216 out of 238 taxa (91%) had at least basic support for a given node. For 35 of these species, the node placement was in an unresolved portion of the tree, mostly including non-foliicolous species of *Gyalideopsis* and relatives for which no sequenced taxon was in the reference tree; three further species of *Gyalideopsis* were placed with the outgroup, suggesting that the reference data set included no closely related taxa for these species. The remaining species were binned into one of the 35 genera in the reference tree. For 22 species (9%), the placement remained unresolved (Table 1; Fig. 2).

Most placements obtained by phylogenetic binning were consistent with anticipated placements from earlier studies, but for a small portion of the taxa (about 10%), the binning results were conflicting with their current or predicted placement (Table 1; Appendix 4). Most of these represented the genus *Gyalideopsis*, the largest genus in the family with over 100 species but for which only few sequenced reference taxa were available and for which a revised genus concept remains unclear. Others included presumably non-sequenced clades, such as *Aplanocalenia inconspicua* (Müll. Arg.) Lücking, Sérus. & Vězda, *Ferraroa hyalina* (Lücking) Lücking, Sérus. & Vězda, *Hippocrepidea nigra* Sérus., and *Paratricharia paradoxa* (Lücking) Lücking, which clustered with *Calenia s.lat.*, *Batistomyces* Xavier-Leite, M.Cáceres & Lücking, *Gyalectidium*, and *Caleniella* Xavier-Leite, M.Cáceres & Lücking, respectively (Table 1). A surprising result was the binning of *Aderkomyces couepiae* Bat., the type of that genus, with the type of *Arthotheliopsis* Vain., *A. hymenocarpoides* Vain., and not with the clade presumed to represent the genus *Aderkomyces*, represented by the sequenced species *A. papilliferus* (Lücking) Lücking, Sérus. & Vězda and two undescribed species (Table 1; Appendix 4). About 50 taxa, roughly one fourth of the taxon sampling, were placed in one of the 16 newly recognized genera included in the reference tree, based on our broader phylogenetic analysis (Xavier-Leite *et al.* 2022). These have been formally recombined into the new genera in a parallel paper (Xavier-Leite *et al.* 2023).

DISCUSSION

Gomphillaceae is a highly diverse family of lichenized fungi, with a potentially high number of yet unrecognized, partially cryptic species (Xavier-Leite *et al.* 2022). Even considering the large set of 223 phenotype characters scored here for this family (based on Lücking *et al.* 2005), Gomphillaceae is not well understood in terms of its internal classification and the usefulness of phenotype characters to delimit genera and species. Studies on this family continue to discover new species and genera on a regular basis (Lücking *et al.* 2007; Lücking 2008; Menezes *et al.* 2013; Lücking *et al.* 2017; Etayo 2017; Lendemer 2017; Xavier-Leite *et al.* 2018; Herrera-Campos *et al.* 2019; Gutteres *et al.* 2020; Roux *et al.* 2022). For better-sampled species complexes, the most recent molecular phylogeny (Xavier-Leite *et al.* 2022) is an indication of the taxonomic diversity in the family, revealing a great deal of hidden diversity in presumably known taxa, such as *Gyalectidium filicinum* Müll. Arg. and *Microxyphiomyces* (*Tricharia*) *vainioi* (R.Sant.) Xavier-Leite, M.Cáceres & Lücking.

This situation is comparable with Graphidaceae, which traditionally comprised 12 genera in two families and now contains over 80 genera and well over 2000 species (Rivas Plata *et al.* 2012a; Lücking *et al.* 2017; Miranda-González *et al.* 2020), with over 3500 predicted (Lücking *et al.* 2014). Since genera should represent clades (i.e., monophyletic groups), but as rank-based units are abstract entities, the

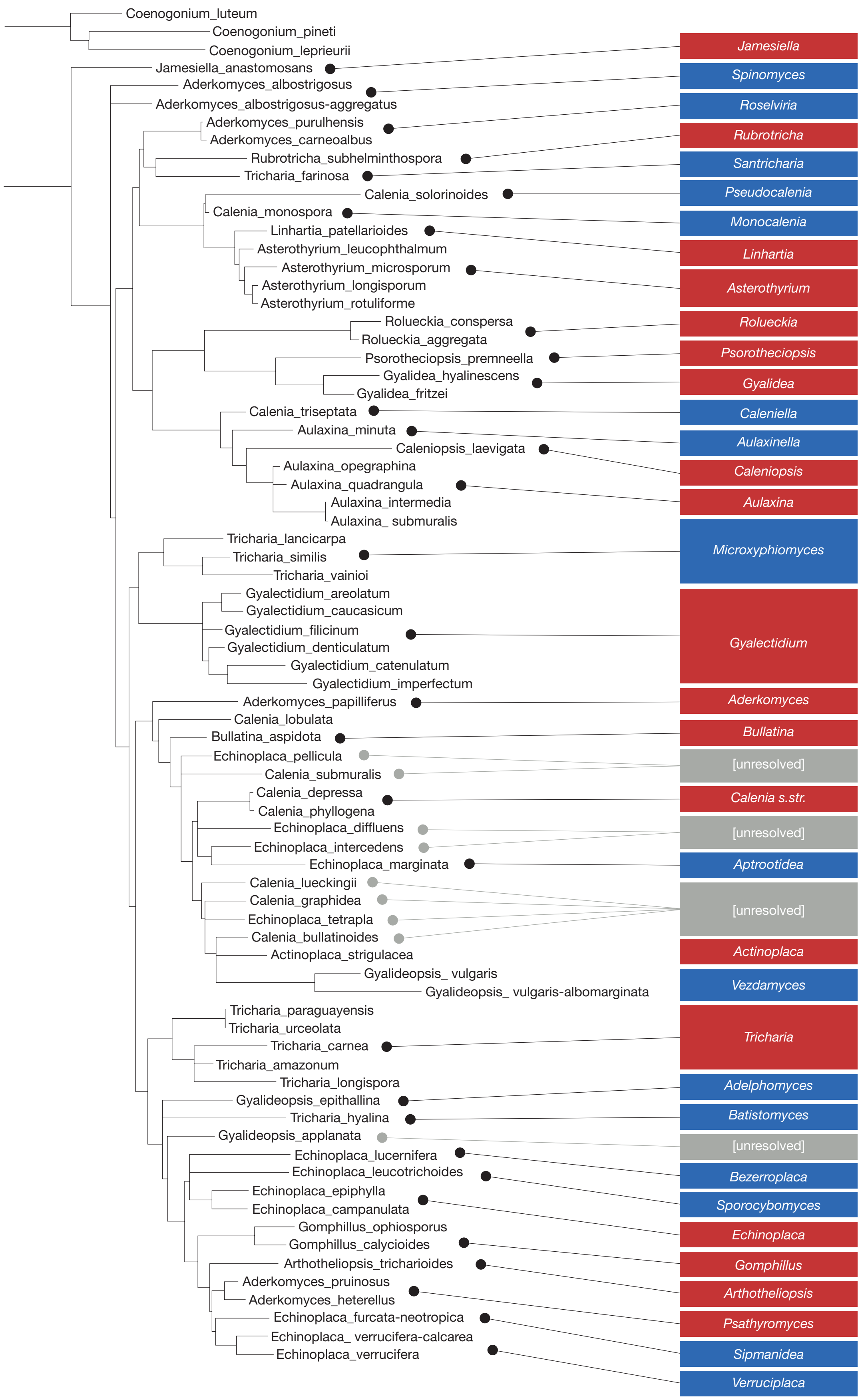

Fig. 1. — The molecular reference tree (maximum likelihood tree) showing 35 genus-level lineages of Gomphillaceae Walt. Watson ex Hafellner and the relationships among genera. The molecular phylogenetic analysis resulted in 13 new genera and three newly reinstated genera for the family (**marked in blue**).

Table 1. — Result of the phylogenetic binning for the 238 query taxa in relation to the 75 reference taxa. Taxa are listed in alphabetical order and for each taxon, all alternative node placements are given, in descending order of support. Node identifications (**ID**) are listed for each node and the final genus placement is indicated for each species; genus placement is necessarily consistent with Node ID for placements with low support. In cases where the placement was not resolved or conflict was detected, we adopted a conservative genus placement (**indicated in brackets**). The table is also available in spreadsheet format (Appendix 4).

Taxon	Node	Support	Node ID	Genus placement
Actinoplaca strigulacea	I90	[ref]	*Actinoplaca*	*Actinoplaca*
Aderkomyces albostrigosus	I3	[ref]	*Spinomyces*	*Spinomyces*
Aderkomyces albostrigosus f. *aggregatus*	I4	[ref]	*Spinomyces*	*Spinomyces*
Aderkomyces armatus	I118	100	*Gyalideopsis applanata* clade	[*Aderkomyces*]
Aderkomyces carneoalbus	I11	[ref]	*Roselviria*	*Roselviria*
Aderkomyces couepiae	I125	100	*Arthotheliopsis*	[*Aderkomyces*]
Aderkomyces cretaceus	I1	100	unresolved	[*Aderkomyces*]
Aderkomyces cubanus	I1	100	unresolved	[*Aderkomyces*]
Aderkomyces deslooveri	I2	100	*Spinomyces*	*Spinomyces*
Aderkomyces dilatatus	I71	100	*Aderkomyces s.str.*	*Aderkomyces*
Aderkomyces fumosus	I1	100	unresolved	[*Aderkomyces*]
Aderkomyces guatemalensis	I2	96	*Spinomyces*	*Spinomyces*
Aderkomyces guatemalensis	I1	4	unresolved	*Spinomyces*
Aderkomyces heterellus	I134	[ref]	*Psathyromyces*	*Psathyromyces*
Aderkomyces lobulicarpus	I9	50	*Roselviria*	*Roselviria*
Aderkomyces lobulicarpus	I11	34	*Roselviria*	*Roselviria*
Aderkomyces lobulicarpus	I106	16	*Tricharia*	*Roselviria*
Aderkomyces microcarpus	I2	100	*Spinomyces*	*Spinomyces*
Aderkomyces microtrichus	I101	99	*Calenia-Echinoplaca* grade	[*Calenia*]
Aderkomyces microtrichus	I141	1	*Echinoplaca*	[*Calenia*]
Aderkomyces papilliferus	I71	[ref]	*Aderkomyces s.str.*	*Aderkomyces*
Aderkomyces planus	I134	100	*Psathyromyces*	*Psathyromyces*
Aderkomyces pruinosus	I133	[ref]	*Psathyromyces*	*Psathyromyces*
Aderkomyces purulhensis	I10	[ref]	*Roselviria*	*Roselviria*
Aderkomyces ramiferus	I1	100	unresolved	[*Aderkomyces*]
Aderkomyces subalbostrigosus	I118	99	*Gyalideopsis applanata* clade	[*Gyalideopsis*]
Aderkomyces subalbostrigosus	I53	1	*Microxyphiomyces*	[*Gyalideopsis*]
Aderkomyces subplanus	I1	100	unresolved	[*Aderkomyces*]
Aderkomyces verruciferus	I126	53	*Verruciplaca*	[*Aderkomyces*]
Aderkomyces verruciferus	I127	29	*Verruciplaca*	[*Aderkomyces*]
Aderkomyces verruciferus	I132	8	*Psathyromyces*	[*Aderkomyces*]
Aderkomyces verruciferus	I2	8	*Spinomyces*	[*Aderkomyces*]
Aderkomyces verruciferus	I118	2	*Gyalideopsis applanata* clade	[*Aderkomyces*]
Aderkomyces verrucosus	I2	100	*Spinomyces*	*Spinomyces*
Arthotheliopsis hymenocarpoides	I125	100	*Arthotheliopsis*	*Arthotheliopsis*
Arthotheliopsis planicarpus	I125	100	*Arthotheliopsis*	*Arthotheliopsis*
Arthotheliopsis serusiauxii	I125	100	*Arthotheliopsis*	*Arthotheliopsis*
Arthotheliopsis tricharioides	I125	[ref]	*Arthotheliopsis*	*Arthotheliopsis*
Asterothyrium anomalum	I26	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium argenteum	I24	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium aspidospermatis	I26	82	*Asterothyrium*	*Asterothyrium*
Asterothyrium aspidospermatis	I31	18	*Psorotheciopsis*	*Asterothyrium*
Asterothyrium atromarginatum	I27	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium aulaxinoides	I25	99	*Asterothyrium*	*Asterothyrium*
Asterothyrium aulaxinoides	I24	1	*Asterothyrium*	*Asterothyrium*
Asterothyrium bisporum	I26	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium chroodisciforme	I25	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium decipiens	I24	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium filiforme	I31	100	*Psorotheciopsis*	[*Asterothyrium*]
Asterothyrium gigantosporum	I25	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium gyalideoides	I20	100	*Linhartia*	[*Asterothyrium*]
Asterothyrium hedbergii	I24	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium leptosporum	I22	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium leucophthalmum	I22	[ref]	*Asterothyrium*	*Asterothyrium*
Asterothyrium longisporum	I25	[ref]	*Asterothyrium*	*Asterothyrium*
Asterothyrium microsporum	I27	[ref]	*Asterothyrium*	*Asterothyrium*
Asterothyrium monosporum	I25	53	*Asterothyrium*	*Asterothyrium*
Asterothyrium monosporum	I26	47	*Asterothyrium*	*Asterothyrium*
Asterothyrium octomerum	I26	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium pallidum	I26	52	*Asterothyrium*	*Asterothyrium*
Asterothyrium pallidum	I25	48	*Asterothyrium*	*Asterothyrium*
Asterothyrium pernambucense	I26	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium pittieri	I25	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium rondoniense	I25	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium rostratum	I27	58	*Asterothyrium*	*Asterothyrium*
Asterothyrium rostratum	I26	42	*Asterothyrium*	*Asterothyrium*
Asterothyrium rotuliforme	I26	[ref]	*Asterothyrium*	*Asterothyrium*

Table 1. — Continuation.

Taxon	Node	Support	Node ID	Genus placement
Asterothyrium segmentatum	I19	81	*Asterothyrium-Linhartia*	[*Asterothyrium*]
Asterothyrium segmentatum	I26	19	*Asterothyrium*	[*Asterothyrium*]
Asterothyrium septemseptatum	I26	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium subargenteum	I27	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium tetrasporum	I25	99	*Asterothyrium*	*Asterothyrium*
Asterothyrium tetrasporum	I24	1	*Asterothyrium*	*Asterothyrium*
Asterothyrium umbilicatum	I31	100	*Psorotheciopsis*	[*Asterothyrium*]
Asterothyrium uniseptatum	I25	100	*Asterothyrium*	*Asterothyrium*
Asterothyrium vezdae	I26	100	*Asterothyrium*	*Asterothyrium*
Aulaxina aggregata	I45	78	*Aulaxina*	*Aulaxina*
Aulaxina aggregata	I115	22	*Adelphomyces*	*Aulaxina*
Aulaxina corticola	I44	100	*Aulaxina*	*Aulaxina*
Aulaxina dictyospora	I50	100	*Aulaxina*	*Aulaxina*
Aulaxina epiphylla	I45	100	*Aulaxina*	*Aulaxina*
Aulaxina intermedia	I49	[ref]	*Aulaxina*	*Aulaxina*
Aulaxina microphana	I44	99	*Aulaxina*	*Aulaxina*
Aulaxina microphana	I42	1	*Aulaxina*	*Aulaxina*
Aulaxina minuta	I41	[ref]	*Aulaxinella*	*Aulaxinella*
Aulaxina multiseptata	I44	100	*Aulaxina*	*Aulaxina*
Aulaxina opegraphina	I45	[ref]	*Aulaxina*	*Aulaxina*
Aulaxina quadrangula	I47	[ref]	*Aulaxina*	*Aulaxina*
Aulaxina submuralis	I50	[ref]	*Aulaxina*	*Aulaxina*
Aulaxina uniseptata	I41	100	*Aulaxinella*	*Aulaxinella*
Aulaxina unispora	I45	100	*Aulaxina*	*Aulaxina*
Bullatina aspidota	I75	[ref]	*Bullatina*	*Bullatina*
Calenia africana	I86	100	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia applanata	I90	100	*Actinoplaca*	[*Aplanocalenia*]
Calenia areolata	I79	100	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia bullatinoides	I88	[ref]	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia depressa	I96	[ref]	*Calenia-Echinoplaca* grade	*Calenia*
Calenia dictyospora	I76	100	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia echinoplacoides	I86	99	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia echinoplacoides	I73	1	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia flava	I77	90	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia flava	I97	5	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia flava	I96	4	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia flava	I79	1	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia fumosa	I86	100	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia graphidea	I84	[ref]	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia inconspicua	I77	43	*Calenia-Echinoplaca* grade	*Aplanocalenia*
Calenia inconspicua	I16	32	*Monocalenia*	*Aplanocalenia*
Calenia inconspicua	I18	16	*Monocalenia*	*Aplanocalenia*
Calenia inconspicua	I90	9	*Actinoplaca*	*Aplanocalenia*
Calenia leptocarpa	I96	49	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia leptocarpa	I77	40	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia leptocarpa	I80	9	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia leptocarpa	I98	2	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia lobulata	I73	[ref]	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia lueckingii	I82	[ref]	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia maculans	I39	100	*Caleniella*	*Caleniella*
Calenia microcarpa	I58	100	*Gyalectidium*	*Gyalectidium*
Calenia minuta	I89	86	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia minuta	I88	11	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia minuta	I91	3	*Vezdamyces*	[*Calenia*]
Calenia monospora	I18	[ref]	*Monocalenia*	*Monocalenia*
Calenia obtecta	I76	100	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia philippinensis	I79	100	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia phyllogena	I97	[ref]	*Calenia-Echinoplaca* grade	*Calenia*
Calenia pruinosa	I73	100	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia rionigrensis	I79	100	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia rolandiana	I16	86	*Monocalenia*	*Monocalenia*
Calenia rolandiana	I28	14	unresolved	*Monocalenia*
Calenia solorinoides	I17	[ref]	*Pseudocalenia*	*Pseudocalenia*
Calenia subdepressa	I86	53	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia subdepressa	I79	47	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia submuralis	I79	[ref]	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia thelotremella	I79	97	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia thelotremella	I97	3	*Calenia-Echinoplaca* grade	[*Calenia*]
Calenia triseptata	I39	[ref]	*Caleniella*	*Caleniella*
Calenia viridis	I18	100	*Monocalenia*	*Monocalenia*

Table 1. — Continuation.

Taxon	Node	Support	Node ID	Genus placement
Caleniopsis laevigata	I43	[ref]	*Caleniopsis*	*Caleniopsis*
Caleniopsis tetramera	I43	100	*Caleniopsis*	*Caleniopsis*
Coenogonium leprieurii	I146	[ref]	outgroup	[outgroup]
Coenogonium luteum	I143	[ref]	outgroup	[outgroup]
Coenogonium pineti	I145	[ref]	outgroup	[outgroup]
Diploschistella athalloides	I14	50	*Santricharia*	[*Diploschistella*]
Diploschistella athalloides	I32	50	*Gyalidea*	[*Diploschistella*]
Diploschistella lithophila	I14	57	*Santricharia*	[*Diploschistella*]
Diploschistella lithophila	I1	41	unresolved	[*Diploschistella*]
Diploschistella lithophila	I32	2	*Gyalidea*	[*Diploschistella*]
Diploschistella solorinellaeformis	I32	100	*Gyalidea*	[*Diploschistella*]
Diploschistella trapperi	I102	96	*Aptrootidea*	[*Diploschistella*]
Diploschistella trapperi	I32	3	*Gyalidea*	[*Diploschistella*]
Diploschistella trapperi	I118	1	*Gyalideopsis applanata* clade	[*Diploschistella*]
Diploschistella urceolata	I1	100	unresolved	[*Diploschistella*]
Echinoplaca amapensis	I102	100	*Aptrootidea*	*Aptrootidea*
Echinoplaca atrofusca	I44	86	*Aulaxina*	[*Aptrootidea*]
Echinoplaca atrofusca	I102	14	*Aptrootidea*	*Aptrootidea*
Echinoplaca atromuralis	I102	100	*Aptrootidea*	*Aptrootidea*
Echinoplaca bispora	I121	100	*Gomphillus*	[*Gyalideopsis*]
Echinoplaca campanulata	I141	[ref]	*Echinoplaca*	*Echinoplaca*
Echinoplaca diffluens	I99	[ref]	*Calenia-Echinoplaca* grade	[*Echinoplaca*]
Echinoplaca epiphylla	I140	[ref]	*Echinoplaca*	*Echinoplaca*
Echinoplaca epiphylloides	I77	98	*Calenia-Echinoplaca* grade	[*Calenia*]
Echinoplaca epiphylloides	I140	2	*Echinoplaca*	[*Calenia*]
Echinoplaca furcata	I129	100	*Verruciplaca*	*Sipmanidea*
Echinoplaca furcata subsp. neotropica	I128	[ref]	*Verruciplaca*	*Sipmanidea*
Echinoplaca fusconitida	I137	100	*Bezerroplaca*	*Bezerroplaca*
Echinoplaca gemmifera	I90	100	*Actinoplaca*	*Actinoplaca*
Echinoplaca handelii	I140	94	*Echinoplaca*	*Echinoplaca*
Echinoplaca handelii	I77	6	*Calenia-Echinoplaca* grade	*Echinoplaca*
Echinoplaca hispida	I77	100	*Calenia-Echinoplaca* grade	[*Calenia*]
Echinoplaca incrustatociliata	I137	91	*Bezerroplaca*	*Bezerroplaca*
Echinoplaca incrustatociliata	I138	6	*Sporocybomyces*	*Bezerroplaca*
Echinoplaca incrustatociliata	I136	3	*Calenia-Echinoplaca* grade	*Bezerroplaca*
Echinoplaca intercedens	I101	[ref]	*Calenia-Echinoplaca* grade	[*Calenia*]
Echinoplaca leucomuralis	I138	100	*Sporocybomyces*	*Sporocybomyces*
Echinoplaca leucotrichoides	I138	[ref]	*Sporocybomyces*	*Sporocybomyces*
Echinoplaca lucernifera	I137	[ref]	*Bezerroplaca*	*Bezerroplaca*
Echinoplaca macgregorii	I138	100	*Sporocybomyces*	*Sporocybomyces*
Echinoplaca madagascariensis	I101	98	*Calenia-Echinoplaca* grade	[*Calenia*]
Echinoplaca madagascariensis	I90	2	*Actinoplaca*	[*Calenia*]
Echinoplaca marginata	I102	[ref]	*Aptrootidea*	*Aptrootidea*
Echinoplaca melanothrix	I136	70	*Calenia-Echinoplaca* grade	[*Echinoplaca*]
Echinoplaca melanothrix	I135	25	*Calenia-Echinoplaca* grade	[*Echinoplaca*]
Echinoplaca melanothrix	I140	4	*Echinoplaca*	[*Echinoplaca*]
Echinoplaca melanothrix	I139	1	*Echinoplaca*	[*Echinoplaca*]
Echinoplaca pachyparaphysata	I137	100	*Bezerroplaca*	*Bezerroplaca*
Echinoplaca pellicula	I77	[ref]	*Calenia-Echinoplaca* grade	[*Calenia*]
Echinoplaca purpurea	I136	68	*Calenia-Echinoplaca* grade	[*Echinoplaca*]
Echinoplaca purpurea	I135	32	*Calenia-Echinoplaca* grade	[*Echinoplaca*]
Echinoplaca similis	I140	98	*Echinoplaca*	[*Echinoplaca*]
Echinoplaca similis	I121	2	*Gomphillus*	[*Echinoplaca*]
Echinoplaca streimannii	I137	100	*Bezerroplaca*	*Bezerroplaca*
Echinoplaca subsimilis	I121	100	*Gomphillus*	[*Gyalideopsis*]
Echinoplaca tetrapla	I86	[ref]	*Calenia-Echinoplaca* grade	[*Calenia*]
Echinoplaca triseptata	I102	100	*Aptrootidea*	*Aptrootidea*
Echinoplaca verrucifera	I131	[ref]	*Verruciplaca*	*Sipmanidea*
Echinoplaca verrucifera f. calcarea	I130	[ref]	*Verruciplaca*	*Sipmanidea*
Echinoplaca vezdana	I99	100	*Calenia-Echinoplaca* grade	[*Echinoplaca*]
Echinoplaca wilsonii	I44	100	*Aulaxina*	*Aptrootidea*
Epilithia cristata	I125	76	*Arthotheliopsis*	[*Gyalideopsis*]
Epilithia cristata	I141	14	*Echinoplaca*	[*Gyalideopsis*]
Epilithia cristata	I32	10	*Gyalidea*	[*Gyalideopsis*]
Gomphillus americanus	I122	100	*Gomphillus*	*Gomphillus*
Gomphillus calycioides	I123	[ref]	*Gomphillus*	*Gomphillus*
Gomphillus ophiosporus	I122	[ref]	*Gomphillus*	*Gomphillus*
Gyalectidium areolatum	I160	[ref]	*Gyalectidium*	*Gyalectidium*
Gyalectidium atrosquamulatum	I68	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium aurelii	I68	100	*Gyalectidium*	*Gyalectidium*

Table 1. — Continuation.

Taxon	Node	Support	Node ID	Genus placement
Gyalectidium australe	I61	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium barbatum	I68	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium catenulatum	I167	[ref]	*Gyalectidium*	*Gyalectidium*
Gyalectidium caucasicum	I161	[ref]	*Gyalectidium*	*Gyalectidium*
Gyalectidium ciliatum	I61	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium colchicum	I65	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium conchiferum	I67	64	*Gyalectidium*	*Gyalectidium*
Gyalectidium conchiferum	I65	32	*Gyalectidium*	*Gyalectidium*
Gyalectidium conchiferum	I68	4	*Gyalectidium*	*Gyalectidium*
Gyalectidium corticola	I82	98	*Calenia-Echinoplaca* grade	[*Calenia*]
Gyalectidium corticola	I73	2	*Calenia-Echinoplaca* grade	[*Calenia*]
Gyalectidium denticulatum	I165	[ref]	*Gyalectidium*	*Gyalectidium*
Gyalectidium eskuchei	I65	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium fantasticum	I60	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium filicinum	I163	[ref]	*Gyalectidium*	*Gyalectidium*
Gyalectidium filicinum-lobatum	I63	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium flabellatum	I61	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium fuscum	I68	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium gahavisukanum	I61	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium imperfectum	I168	[ref]	*Gyalectidium*	*Gyalectidium*
Gyalectidium kenyanum	I65	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium laciniatum	I65	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium maracae	I65	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium membranaceum	I68	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium minus	I68	88	*Gyalectidium*	*Gyalectidium*
Gyalectidium minus	I61	12	*Gyalectidium*	*Gyalectidium*
Gyalectidium novoguineense	I61	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium pallidum	I65	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium palmicola	I60	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium puntilloi	I60	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium radiatum	I65	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium setiferum	I65	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium ulloae	I65	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium verruculosum	I65	100	*Gyalectidium*	*Gyalectidium*
Gyalectidium yahriae	I65	100	*Gyalectidium*	*Gyalectidium*
Gyalidea fritzei	I34	[ref]	*Gyalidea*	*Gyalidea*
Gyalidea hyalinescens	I33	[ref]	*Gyalidea*	*Gyalidea*
Gyalideopsis actinoplacoides	I118	100	*Gyalideopsis applanata* clade	[*Gyalideopsis*]
Gyalideopsis aequatoriana	I121	100	*Gomphillus*	[*Gyalideopsis*]
Gyalideopsis africana	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis albopruinosa	I11	100	*Roselviria*	[*Gyalideopsis*]
Gyalideopsis applanata	I118	[ref]	*Gyalideopsis applanata* clade	[*Gyalideopsis*]
Gyalideopsis argentea	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis bispora	I1	97	unresolved	[*Gyalideopsis*]
Gyalideopsis bispora	I107	3	*Tricharia*	[*Gyalideopsis*]
Gyalideopsis brevipilosa	I121	53	*Gomphillus*	[*Gyalideopsis*]
Gyalideopsis brevipilosa	I1	47	unresolved	[*Gyalideopsis*]
Gyalideopsis buckei	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis bullata	I118	100	*Gyalideopsis applanata* clade	[*Gyalideopsis*]
Gyalideopsis calabrica	I143	97	outgroup	[*Gyalideopsis*]
Gyalideopsis calabrica	I1	3	unresolved	[*Gyalideopsis*]
Gyalideopsis capitata	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis choshuencensis	I118	100	*Gyalideopsis applanata* clade	[*Gyalideopsis*]
Gyalideopsis cochlearifera	I115	100	*Adelphomyces*	*Adelphomyces*
Gyalideopsis confluens	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis cyanophila	I121	100	*Gomphillus*	[*Gyalideopsis*]
Gyalideopsis epithallina	I115	[ref]	*Adelphomyces*	*Adelphomyces*
Gyalideopsis floridae	I142	96	outgroup	[*Gyalideopsis*]
Gyalideopsis floridae	I1	4	unresolved	[*Gyalideopsis*]
Gyalideopsis formosana	I1	62	unresolved	[*Gyalideopsis*]
Gyalideopsis formosana	I32	37	*Gyalidea*	[*Gyalideopsis*]
Gyalideopsis formosana	I9	1	*Roselviria*	[*Gyalideopsis*]
Gyalideopsis gigantea	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis giganteoides	I134	100	*Psathyromyces*	[*Gyalideopsis*]
Gyalideopsis haliotidiformis	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis helvetica	I121	80	*Gomphillus*	[*Gyalideopsis*]
Gyalideopsis helvetica	I142	20	outgroup	[*Gyalideopsis*]
Gyalideopsis hyalina	I116	100	*Batistomyces*	[*Ferraroa*]
Gyalideopsis intermedia	I11	100	*Roselviria*	[*Gyalideopsis*]
Gyalideopsis japonica	I1	100	unresolved	[*Gyalideopsis*]

Table 1. — Continuation.

Taxon	Node	Support	Node ID	Genus placement
Gyalideopsis kalbii	I13	77	*Rubrotricha*	[*Gyalideopsis*]
Gyalideopsis kalbii	I1	23	unresolved	[*Gyalideopsis*]
Gyalideopsis krogiae	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis laevithallina	I11	100	*Roselviria*	[*Gyalideopsis*]
Gyalideopsis lambinonii	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis lecideina	I14	63	*Santricharia*	[*Gyalideopsis*]
Gyalideopsis lecideina	I1	37	unresolved	[*Gyalideopsis*]
Gyalideopsis lobulata	I10	100	*Roselviria*	[*Gyalideopsis*]
Gyalideopsis megalospora	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis mexicana	I121	99	*Gomphillus*	[*Gyalideopsis*]
Gyalideopsis mexicana	I1	1	unresolved	[*Gyalideopsis*]
Gyalideopsis minima	I56	100	*Microxyphiomyces*	[*Gyalideopsis*]
Gyalideopsis minutissima	I115	87	*Adelphomyces*	[*Gyalideopsis*]
Gyalideopsis minutissima	I13	13	*Rubrotricha*	[*Gyalideopsis*]
Gyalideopsis modesta	I32	100	*Gyalidea*	[*Gyalideopsis*]
Gyalideopsis monospora	I106	100	*Tricharia*	[*Gyalideopsis*]
Gyalideopsis montana	I91	64	*Vezdamyces*	[*Gyalideopsis*]
Gyalideopsis montana	I11	31	*Roselviria*	[*Gyalideopsis*]
Gyalideopsis montana	I93	5	*Vezdamyces*	[*Gyalideopsis*]
Gyalideopsis muscicola	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis napoensis	I121	64	*Gomphillus*	[*Gyalideopsis*]
Gyalideopsis napoensis	I118	36	*Gyalideopsis applanata* clade	[*Gyalideopsis*]
Gyalideopsis nepalensis	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis ochroleuca	I11	79	*Roselviria*	[*Gyalideopsis*]
Gyalideopsis ochroleuca	I10	16	*Roselviria*	[*Gyalideopsis*]
Gyalideopsis ochroleuca	I4	5	*Spinomyces*	[*Gyalideopsis*]
Gyalideopsis pallescens	I11	98	*Roselviria*	[*Gyalideopsis*]
Gyalideopsis pallescens	I9	2	*Roselviria*	[*Gyalideopsis*]
Gyalideopsis pallida	I13	87	*Rubrotricha*	[*Gyalideopsis*]
Gyalideopsis pallida	I115	12	*Adelphomyces*	[*Gyalideopsis*]
Gyalideopsis pallida	I19	1	*Asterothyrium-Linhartia*	[*Gyalideopsis*]
Gyalideopsis palmata	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis parvula	I115	100	*Adelphomyces*	*Adelphomyces*
Gyalideopsis perminuta	I13	99	*Rubrotricha*	[*Gyalideopsis*]
Gyalideopsis perminuta	I56	1	*Microxyphiomyces*	[*Gyalideopsis*]
Gyalideopsis peruviana	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis philippiae	I142	100	outgroup	[*Gyalideopsis*]
Gyalideopsis piceicola	I1	95	unresolved	[*Gyalideopsis*]
Gyalideopsis piceicola	I142	5	outgroup	[*Gyalideopsis*]
Gyalideopsis puertoricensis	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis robusta	I106	90	*Tricharia*	[*Gyalideopsis*]
Gyalideopsis robusta	I112	10	*Tricharia*	[*Gyalideopsis*]
Gyalideopsis rogersii	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis rostrata	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis rubescens	I57	100	*Microxyphiomyces*	[*Gyalideopsis*]
Gyalideopsis rubra	I1	97	unresolved	[*Gyalideopsis*]
Gyalideopsis rubra	I14	3	*Santricharia*	[*Gyalideopsis*]
Gyalideopsis rubrofusca	I0	100	*Jamesiella*	[*Gyalideopsis*]
Gyalideopsis stipitata	I1	98	unresolved	[*Gyalideopsis*]
Gyalideopsis stipitata	I112	2	*Tricharia*	[*Gyalideopsis*]
Gyalideopsis subantarctica	I32	100	*Gyalidea*	[*Gyalideopsis*]
Gyalideopsis triseptata	I56	99	*Microxyphiomyces*	[*Gyalideopsis*]
Gyalideopsis triseptata	I115	1	*Adelphomyces*	[*Gyalideopsis*]
Gyalideopsis vainioi	I106	80	*Tricharia*	[*Gyalideopsis*]
Gyalideopsis vainioi	I1	15	unresolved	[*Gyalideopsis*]
Gyalideopsis vainioi	I121	5	*Gomphillus*	[*Gyalideopsis*]
Gyalideopsis verruculosa	I52	56	*Microxyphiomyces*	[*Gyalideopsis*]
Gyalideopsis verruculosa	I107	42	*Tricharia*	[*Gyalideopsis*]
Gyalideopsis verruculosa	I13	2	*Rubrotricha*	[*Gyalideopsis*]
Gyalideopsis vezdae	I1	100	unresolved	[*Gyalideopsis*]
Gyalideopsis vulgaris	I92	[ref]	*Vezdamyces*	*Vezdamyces*
Gyalideopsis vulgaris f. *albopruinosa*	I93	[ref]	*Vezdamyces*	*Vezdamyces*
Gyalideopsis williamsii	I1	76	unresolved	[*Gyalideopsis*]
Gyalideopsis williamsii	I112	23	*Tricharia*	[*Gyalideopsis*]
Gyalideopsis williamsii	I4	1	*Spinomyces*	[*Gyalideopsis*]
Gyalideopsis wirthii	I11	67	*Roselviria*	[*Gyalideopsis*]
Gyalideopsis wirthii	I1	20	unresolved	[*Gyalideopsis*]
Gyalideopsis wirthii	I9	12	*Roselviria*	[*Gyalideopsis*]
Gyalideopsis wirthii	I4	1	*Spinomyces*	[*Gyalideopsis*]
Hippocrepidea nigra	I60	100	*Gyalectidium*	[*Hippocrepidea*]

Table 1. — Continuation.

Taxon	Node	Support	Node ID	Genus placement
Jamesiella anastomosans	I0	[ref]	*Jamesiella*	*Jamesiella*
Jamesiella perlucida	I1	100	unresolved	[*Jamesiella*]
Jamesiella scotica	I1	90	unresolved	[*Jamesiella*]
Jamesiella scotica	I142	10	outgroup	[*Jamesiella*]
Linhartia albomaculans	I31	100	*Psorotheciopsis*	*Psorotheciopsis*
Linhartia guajalitensis	I20	100	*Linhartia*	*Linhartia*
Linhartia gyalideoides	I20	100	*Linhartia*	*Linhartia*
Linhartia patellarioides	I20	[ref]	*Linhartia*	*Linhartia*
Linhartia philippinensis	I20	100	*Linhartia*	*Linhartia*
Linhartia varieseptata	I20	100	*Linhartia*	*Linhartia*
Lithogyalideopsis aterrima	I32	100	*Gyalidea*	[*Lithogyalideopsis*]
Lithogyalideopsis poeltii	I28	58	unresolved	[*Lithogyalideopsis*]
Lithogyalideopsis poeltii	I106	42	*Tricharia*	[*Lithogyalideopsis*]
Lithogyalideopsis vivantii	I32	98	*Gyalidea*	[*Lithogyalideopsis*]
Lithogyalideopsis vivantii	I39	2	*Caleniella*	[*Lithogyalideopsis*]
Lithogyalideopsis zeylandica	I32	79	*Gyalidea*	[*Lithogyalideopsis*]
Lithogyalideopsis zeylandica	I14	21	*Santricharia*	[*Lithogyalideopsis*]
Microlychnus epicorticis	I121	100	*Gomphillus*	[*Gyalideopsis*]
Microspatha glauca	I1	100	unresolved	[*Gyalideopsis*]
Paratricharia paradoxa	I39	99	*Caleniella*	[*Paratricharia*]
Paratricharia paradoxa	I40	1	*Aulaxina*	[*Paratricharia*]
Phallomyces palmae	I125	99	*Arthotheliopsis*	*Aderkomyces*
Phallomyces palmae	I57	1	*Microxyphiomyces*	*Aderkomyces*
Psathyromyces rosacearum	I134	100	*Psathyromyces*	*Psathyromyces*
Psorotheciopsis premneella	I31	[ref]	*Psorotheciopsis*	*Psorotheciopsis*
Rolueckia aggregata	I37	[ref]	*Rolueckia*	*Rolueckia*
Rolueckia conspersa	I36	[ref]	*Rolueckia*	*Rolueckia*
Rubrotricha helminthospora	I13	100	*Rubrotricha*	*Rubrotricha*
Rubrotricha subhelminthospora	I13	[ref]	*Rubrotricha*	*Rubrotricha*
Sporocybomyces pulcher	I138	100	*Sporocybomyces*	*Sporocybomyces*
Tricharia amazonum	I111	[ref]	*Tricharia*	*Tricharia*
Tricharia atrocarpa	I106	100	*Tricharia*	*Tricharia*
Tricharia aulaxiniformis	I115	97	*Adelphomyces*	[*Tricharia*]
Tricharia aulaxiniformis	I41	3	*Aulaxinella*	[*Tricharia*]
Tricharia aulaxinoides	I106	99	*Tricharia*	*Tricharia*
Tricharia aulaxinoides	I112	1	*Tricharia*	*Tricharia*
Tricharia bambusae	I106	100	*Tricharia*	*Tricharia*
Tricharia carnea	I109	[ref]	*Tricharia*	*Tricharia*
Tricharia cuneata	I55	63	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia cuneata	I57	17	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia cuneata	I52	11	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia cuneata	I53	9	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia demoulinii	I56	99	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia demoulinii	I57	1	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia elegans	I56	75	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia elegans	I55	18	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia elegans	I52	5	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia elegans	I53	2	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia elegans (hyphophores)	I55	87	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia elegans (hyphophores)	I52	7	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia elegans (hyphophores)	I53	5	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia elegans (hyphophores)	I57	1	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia farinosa	I14	[ref]	*Santricharia*	*Santricharia*
Tricharia hyalina	I116	[ref]	*Batistomyces*	*Batistomyces*
Tricharia kashiwadanii	I70	70	unresolved	*Microxyphiomyces*
Tricharia kashiwadanii	I54	30	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia lancicarpa	I54	[ref]	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia longispora	I112	[ref]	*Tricharia*	*Tricharia*
Tricharia novoguineense	I115	100	*Adelphomyces*	[*Tricharia*]
Tricharia pallida	I116	76	*Batistomyces*	*Batistomyces*
Tricharia pallida	I9	24	*Roselviria*	*Batistomyces*
Tricharia paraguayensis	I106	[ref]	*Tricharia*	*Tricharia*
Tricharia pseudosantessonii	I116	89	*Batistomyces*	*Batistomyces*
Tricharia pseudosantessonii	I14	10	*Santricharia*	*Batistomyces*
Tricharia pseudosantessonii	I103	1	*Tricharia*	*Batistomyces*
Tricharia santessoniana	I56	74	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia santessoniana	I116	26	*Batistomyces*	*Microxyphiomyces*
Tricharia santessonii	I56	100	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia similis	I56	[ref]	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia sublancicarpa	I106	62	*Tricharia*	*Tricharia*

Table 1. — Continuation.

Taxon	Node	Support	Node ID	Genus placement
Tricharia sublancicarpa	I54	34	*Microxyphiomyces*	*Tricharia*
Tricharia sublancicarpa	I105	3	*Tricharia*	*Tricharia*
Tricharia sublancicarpa	I107	1	*Tricharia*	*Tricharia*
Tricharia substipitata	I112	99	*Tricharia*	*Tricharia*
Tricharia substipitata	I9	1	*Roselviria*	*Tricharia*
Tricharia testacea	I121	72	*Gomphillus*	[*Gyalideopsis*]
Tricharia testacea	I134	22	*Psathyromyces*	[*Gyalideopsis*]
Tricharia testacea	I132	6	*Psathyromyces*	[*Gyalideopsis*]
Tricharia triseptata	I56	100	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia umbrosa	I106	100	*Tricharia*	*Tricharia*
Tricharia urceolata	I107	[ref]	*Tricharia*	*Tricharia*
Tricharia vainioi	I57	[ref]	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia variratae	I56	100	*Microxyphiomyces*	*Microxyphiomyces*
Tricharia vezdae	I1	100	unresolved	[*Gyalideopsis*]

number of genera distinguished in a group is subjective and should be based on practicability, guidelines, and community agreement. One possible guideline is the species-to-genus ratio. In lichen fungi it is currently about 20:1 (Lücking *et al.* 2017; Lücking 2019), comparable to the ratio found in vascular plants but higher than in most animal groups, where it may be as low as 5:1 (Resh & McElravy 1993; Lenat & Resh 2001; Krug *et al.* 2008; Lücking 2019). In Graphidaceae, the current ratio is about 28:1 (Rivas Plata *et al.* 2012a; Rivas Plata *et al.* 2013; Lücking *et al.* 2017), which suggests that Graphidaceae are comparatively under-split at the genus level. With the 46 genera now recognized in Gomphillaceae (Etayo 2017; Lücking *et al.* 2017; Xavier-Leite *et al.* 2022, 2023), the current ratio for this family would be about 10:1, indicating oversplitting compared to lichen fungi overall. However, Gomphillaceae are much understudied; the recent phylogenetic analysis indicated considerable levels of cryptic speciation even in seemingly well-characterized taxa, such as *Gyalectidium* and *Tricharia s.lat.* (Xavier-Leite *et al.* 2022). As a consequence, the true species richness is likely much higher than the currently recognized 440 species. Lücking *et al.* (2014) predicted at least 700 species for this group, but given the level of previously unrecognized cryptic speciation, this prediction is likely conservative and the true number might be well over 800. Thus, the species:genus ratio in the family may approach roughly 20:1 with further species discoveries, the average for lichen fungi in general.

As with Graphidaceae, in Gomphillaceae the challenge with changing classifications based on molecular data, especially in groups were presumed key characters evolved multiple times independently, is the best possible phenotypic circumscription of these genera and the placement of species that lack molecular data. The binning approach provides a solution to this dilemma. However, while phenotype-based phylogenetic binning provides objective and testable predictions for the taxonomic placement of species for which no molecular data is available, it is also dependent on the underlying data and parameters. In the present case, the binning results were largely consistent with expectations, but a portion of the taxa either remained unresolved or was binned into unexpected clades. This was largely caused by the limited taxon sampling in the molecular reference tree, with a strong focus on foliicolous taxa and very few non-foliicolous taxa sequenced, which represent around a quarter of the family. Species of the genus *Gyalideopsis s.lat.* did not perform well with this approach, and due to the very limited sampling of the entirely non-foliicolous genus *Gyalidea*, species of this genus were not binned. The binning approach helps to single out key taxa that need to be targeted for additional sequencing in order to further improve our understanding of the classification of a group such as Gomphillaceae, in this case particularly the two aforementioned genera. On the other hand, we were able to assign about 50 species to 16 of the 19 newly recognized genus level clades distinguished in the previous molecular analysis (Xavier-Leite *et al.* 2022), which also aided in the correct circumscription of these new genera (Xavier-Leite *et al.* 2023).

Thus far, the binning approach has mostly been used in lichen fungi, particularly Gomphillaceae, Graphidaceae, and Roccellaceae (Berger *et al.* 2011b; Rivas Plata *et al.* 2012b; Parnmen *et al.* 2012; Lücking *et al.* 2015; Lücking & Kalb 2018; Perlmutter *et al.* 2020), but also in some animal and plant groups (Koch *et al.* 2012; Fang *et al.* 2013; Springer *et al.* 2015; Dohrmann *et al.* 2017; Testo *et al.* 2018). Most analyses were done in Graphidaceae, which helped to considerably improve predictive classifications, e.g. in the genera *Graphis* versus *Allographa* and in the highly complex tribe Ocellularieae (Berger *et al.* 2011b; Rivas Plata *et al.* 2012b; Lücking *et al.* 2015; Lücking & Kalb 2018). The situation in Gomphillaceae is comparable, with numerous distinctive groups that could be recognized as genera based on molecular and morphological data, but also with unresolved lineages and a large number of unsequenced species (Xavier-Leite *et al.* 2022). Binning cannot only be used to place species in re-defined genera, but also to assess diagnostic characters. For instance, Parnmen *et al.* (2012) used this method to apply quantitative statistics (multiple response permutation procedure, MRPP) to groups defined through the binning approach, in order to evaluate the highest level of phenotype discrimination among re-defined genera in Graphidaceae.

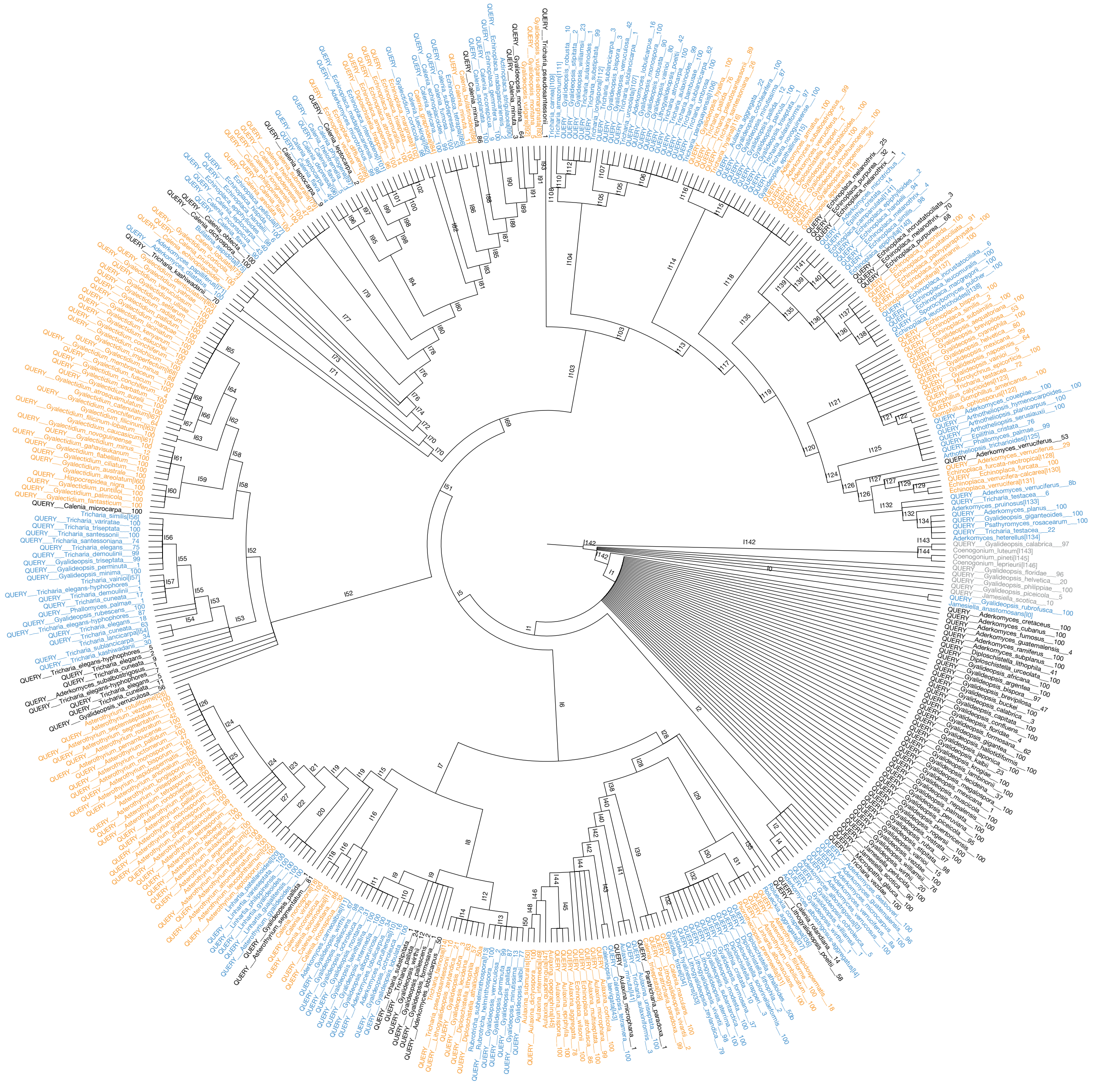

Fig. 2. — Result of the phenotype-based phylogenetic binning using taxa in the molecular reference and taxa based on their phenotype characters. The analysis includes node numbers on each branch and bootstrap support values from the binning approach for each query taxon after the query name. For full tree, see Appendix 5.

This approach will also be useful for Gomphillaceae when more species have been sequenced.

A case study to resolve a taxonomic and nomenclatural problem by evaluating the placement of the type species through binning in Graphidaceae was *Leptotrema* Mont. & Bosch. Lücking *et al.* (2015) found that the type species belonged in the genus *Myriotrema* Fée, whereas the most common species, *L. wightii* (Taylor) Müll. Arg., was unrelated and a new genus was established under the name *Sanguinotrema* Lücking. A somewhat similar situation was found in Gomphillaceae, where Lücking *et al.* (2005) previously separated two genera, *Aderkomyces* and *Arthotheliopsis*, for a group of rather similar species. The expanded phylogenetic analysis (Xavier-Leite *et al.* 2022) showed that two distant clades may correspond to these two genera, but the type of *Aderkomyces*, *A. couepiae*, which so far has not been sequenced, binned with *Arthotheliopsis* based on its phenotype, possibly requiring the description of a new genus for the other clade if this placement is confirmed by molecular data.

Overall, our study is a further example of the usefulness of the phylogenetic binning tool in highly diverse and complex taxonomic groups for which it is difficult to obtain sequence data at a broad taxonomic level. It also revealed the shortcomings of this approach in cases of molecularly unsampled lineages, with the need to obtain additional sequence data for the principally non-foliicolous taxa in the genera *Gyalidea* and *Gyalideopsis s.lat.*

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APPENDICES

Appendix 1. — Characters and character state definitions used in the morphology-based phylogenetic binning analysis, based on Lücking *et al.* (2005) and modified. All characters are binarily coded (**abs**, absent; **pre**, present). The numbers correspond to those used by Lücking *et al.* (2005) and in the present data matrix (see Appendix 4); added characters are marked with **asterisks** at their place of insertion. https://doi.org/10.5852/cryptogamie-mycologie2024v45a8_s1

Appendix 2. — Character matrix for the 310 studied taxa of Gomphillaceae Walt. Watson ex Hafellner and the three outgroup species of *Coenogonium* Ehrenb. For character and character state definitions see Appendix 1. https://doi.org/10.5852/cryptogamie-mycologie2024v45a8_s2

Appendix 3. — Molecular alignment of the mtSSU and nuLSU markers for the 75 reference taxa (including three outgroup species of *Coenogonium* Ehrenb.) in Fasta format. https://doi.org/10.5852/cryptogamie-mycologie2024v45a8_s3

Appendix 4. — Results of the phenotype-based phylogenetic binning analysis for the query taxa. https://doi.org/10.5852/cryptogamie-mycologie2024v45a8_s4

Appendix 5. — Labelled classification tree resulting from phenotype-based phylogenetic binning analysis for the query taxa. https://doi.org/10.5852/cryptogamie-mycologie2024v45a8_s5