

cryptogamie

Mycologie

2024 • 45 • 8

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

Amanda Barreto XAVIER-LEITE, Bruno Tomio GOTO,
Marcela Eugenia da Silva CACERES & Robert LÜCKING

DIRECTEUR DE LA PUBLICATION / PUBLICATION DIRECTOR: Gilles BLOCH
Président du Muséum national d'Histoire naturelle

RÉDACTEUR EN CHEF / EDITOR-IN-CHIEF: Philippe SILAR

ASSISTANT DE RÉDACTION / ASSISTANT EDITOR: Chris LE COQUET-LE ROUX (myco@cryptogamie.com)

MISE EN PAGE / PAGE LAYOUT: Chris LE COQUET-LE ROUX

RÉDACTEURS ASSOCIÉS / ASSOCIATE EDITORS

Slavomír ADAMČÍK

Institute of Botany, Plant Science and Biodiversity Centre, Slovak Academy of Sciences, Dúbravská cesta 9, SK-84523, Bratislava (Slovakia)

Cony DECOCK

Mycothèque de l'Université catholique de Louvain, Earth and Life Institute, Microbiology, Université catholique de Louvain, Croix du Sud 3, B-1348 Louvain-la-Neuve (Belgium)

Damien ERTZ

Meise Botanic Garden, Department Research, Nieuwelaan 38, BE-1860 Meise (Belgium)

André FRAITURE

Botanic Garden Meise, Domein van Bouchout, B-1860 Meise (Belgium)

Kevin D. HYDE

School of Science, Mae Fah Luang University, 333 M. 1 T.Tasud Muang District, Chiang Rai 57100 (Thailand)

Valérie HOFSTETTER

Station de recherche Agroscope Changins-Wädenswil, Dépt. Protection des plantes, Mycologie, CH-1260 Nyon 1 (Switzerland)

Sinang HONGSANAN

College of Life Science and Oceanography, Shenzhen University, 1068, Nanhai Avenue, Nanshan, ShenZhen 518055 (China)

Egon HORAK

Schlossfeld 17, A-6020 Innsbruck (Austria)

Jing LUO

Department of Plant Biology & Pathology, Rutgers University New Brunswick, NJ 08901 (United States)

Ruvishika S. JAYAWARDENA

Center of Excellence in Fungal Research, Mae Fah Luang University, 333 M. 1 T.Tasud Muang District, Chiang Rai 57100 (Thailand)

Chen JIE

Instituto de Ecología, Xalapa 91070, Veracruz (México)

Sajeewa S.N. MAHARCHCHIKUMBURA

Department of Crop Sciences, College of Agricultural and Marine Sciences, Sultan Qaboos University (Oman)

Pierre-Arthur MOREAU

UE 7144. Faculté des Sciences pharmaceutiques et biologiques. Université Lille Nord de France. F-59006 Lille (France)

Tian QING

Center of Excellence in Fungal Research, Mae Fah Luang University 333 M. 1 T.Tasud Muang District, Chiang Rai 57100 (Thailand)

Sylvie RAPIOR

Laboratoire de Botanique, Phytochimie et Mycologie / UMR -CNRS 5175 CEFE, Faculté de Pharmacie, 15, avenue Charles-Flahault, Université Montpellier I, BP 14491, 34093 Montpellier Cedex 5 (France)

Franck RICHARD

Université de Montpellier II, CEFE/CNRS Campus du CNRS, 1919, route de Mende, 34293 Montpellier Cedex 5 (France)

Naritsada THONGKLANG

Center of Excellence in Fungal Research, Mae Fah Luang University, 333 M. 1 T.Tasud Muang District, Chiang Rai 57100 (Thailand)

Xiang-Hua WANG

CAS Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Lanhei Road 132, Kunming 650201, P. R. (China)

COUVERTURE / COVER:

Photograph of *Tricharia longispora* Kalb & Vězda.

Cryptogamie, Mycologie est indexé dans / *Cryptogamie, Mycologie is indexed in:*

- Biological Abstracts
- Current Contents
- Science Citation Index
- Publications bibliographiques du CNRS (Pascal)

Cryptogamie, Mycologie est distribué en version électronique par / *Cryptogamie, Mycologie is distributed electronically by:*

- BioOne® (<http://www.bioone.org/loi/crym>)

Cryptogamie, Mycologie est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Cryptogamie, Mycologie is a fast track journal published by the Museum Science Press, Paris

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish: Adansonia, Geodiversitas, Zoosystema, Anthropozoologica, European Journal of Taxonomy, Naturae, Comptes Rendus Palevol, Cryptogamie sous-sections Algologie, Bryologie.*

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle

CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)

Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40

diff.pub@mnhn.fr / <http://sciencepress.mnhn.fr>

© Publications scientifiques du Muséum national d'Histoire naturelle, Paris, 2024

ISSN (imprimé / print) : 0181-1584 / ISSN (électronique / electronic) : 1776-100

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

Amanda Barreto XAVIER-LEITE

Programa de Pós-Graduação em Sistemática e Evolução, CB,
Universidade Federal do Rio Grande do Norte,
Campus Universitário, 59072-970, Natal, Rio Grande do Norte (Brazil)
amandabxleite@hotmail.com

Bruno Tomio GOTO

Departamento de Botânica e Zoologia, CB, Universidade Federal do Rio Grande do Norte,
Campus Universitário, 59072-970, Natal, Rio Grande do Norte (Brazil)
brunogoto@hotmail.com

Marcela Eugenia da Silva CÁCERES

Departamento de Biociências, Universidade Federal de Sergipe,
Avenida Vereador Olimpio Grande, s/n, Bairro Centro, CEP 49500-000, Itabaiana, Sergipe (Brazil)
mscaceres@hotmail.com

Robert LÜCKING

Botanischer Garten und Botanisches Museum Berlin, Freie Universität Berlin,
Königin-Luise-Strasse 6-8, 14195 Berlin (Germany)
r.luecking@bo.berlin

Submitted on 10 July 2023 | Accepted on 21 December 2023 | Published on 9 August 2024

Xavier-Leite A. B., Goto B. T., Cáceres M. E. da S. & Lücking R. 2024. — Reclassification of species in the lichenized family Gomphillaceae Walt. Watson ex Hafellner (Ascomycota: Graphidales) using morphology-based phylogenetic binning. *Cryptogamie, Mycologie* 45 (8): 83-99. <https://doi.org/10.5252/cryptogamie-mycologie2024v45a8>. <http://cryptogamie.com/mycologie/45/8>

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

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

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.

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 foliicoles,
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 phenotypic 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 downweighted); 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; Gutierrez *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; Gutierrez *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, *Hippocrepeidea 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. hymenocarpoideus* 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; Gutierrez *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

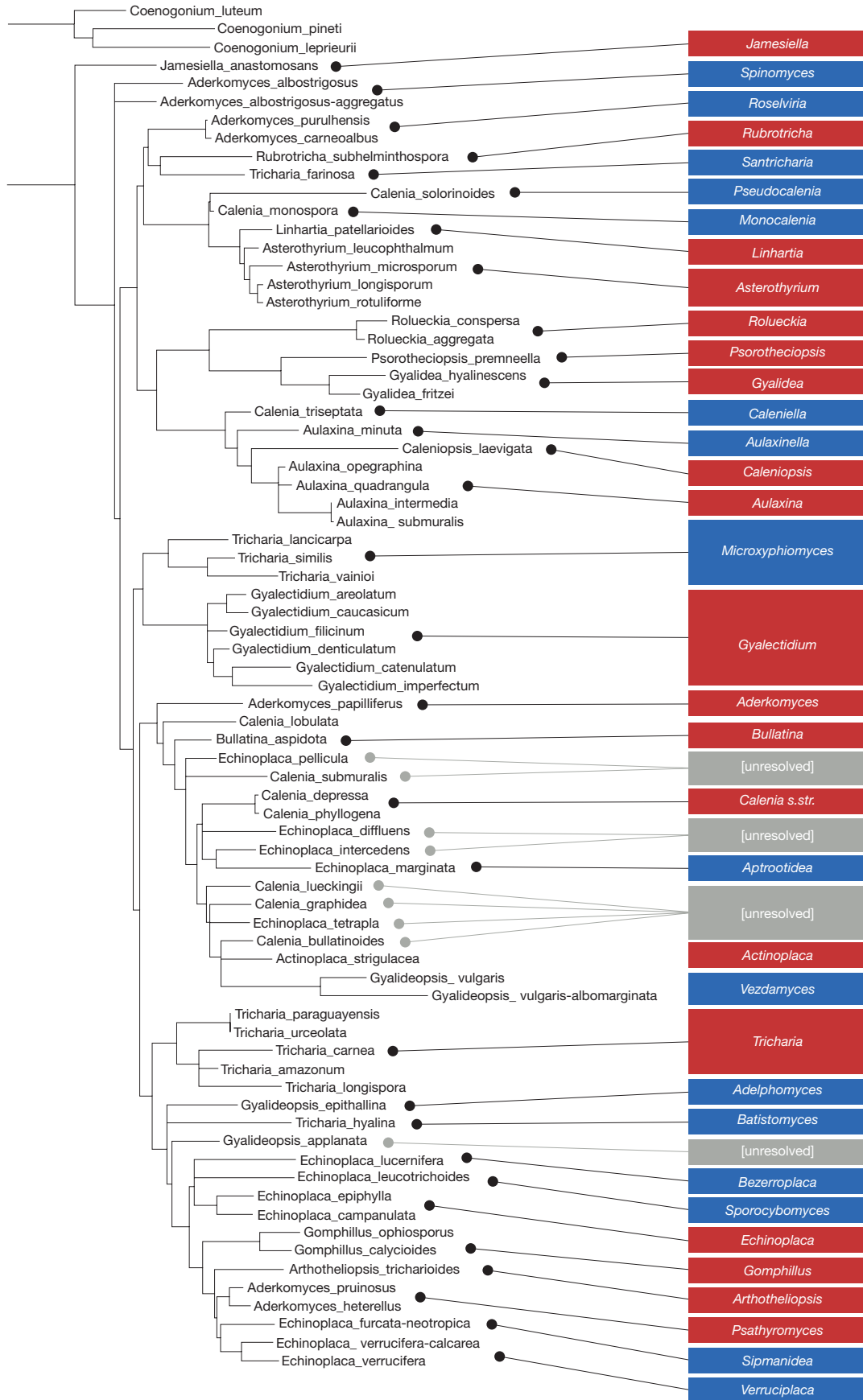


Fig. 1. — The molecular reference tree (maximum likelihood tree) showing 35 genus-level lineages of Gomphillaceae Walt. Watson ex Hafellner and the relationships among genera. The molecular phylogenetic analysis resulted in 13 new genera and three newly reinstated genera for the family (marked in blue).

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

Table 1. — Continuation.

Taxon	Node	Support	Node ID	Genus placement
<i>Asterothyrium segmentatum</i>	l19	81	<i>Asterothyrium-Linhartia</i>	[<i>Asterothyrium</i>]
<i>Asterothyrium segmentatum</i>	l26	19	<i>Asterothyrium</i>	[<i>Asterothyrium</i>]
<i>Asterothyrium septemseptatum</i>	l26	100	<i>Asterothyrium</i>	<i>Asterothyrium</i>
<i>Asterothyrium subargenteum</i>	l27	100	<i>Asterothyrium</i>	<i>Asterothyrium</i>
<i>Asterothyrium tetrasporum</i>	l25	99	<i>Asterothyrium</i>	<i>Asterothyrium</i>
<i>Asterothyrium tetrasporum</i>	l24	1	<i>Asterothyrium</i>	<i>Asterothyrium</i>
<i>Asterothyrium umbilicatum</i>	l31	100	<i>Psorotheciopsis</i>	[<i>Asterothyrium</i>]
<i>Asterothyrium uniseptatum</i>	l25	100	<i>Asterothyrium</i>	<i>Asterothyrium</i>
<i>Asterothyrium vezdae</i>	l26	100	<i>Asterothyrium</i>	<i>Asterothyrium</i>
<i>Aulaxina aggregata</i>	l45	78	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina aggregata</i>	l115	22	<i>Adelphomyces</i>	<i>Aulaxina</i>
<i>Aulaxina corticola</i>	l44	100	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina dictyospora</i>	l50	100	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina epiphylla</i>	l45	100	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina intermedia</i>	l49	[ref]	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina microphana</i>	l44	99	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina microphana</i>	l42	1	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina minuta</i>	l41	[ref]	<i>Aulaxinella</i>	<i>Aulaxinella</i>
<i>Aulaxina multiseptata</i>	l44	100	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina opegraphina</i>	l45	[ref]	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina quadrangula</i>	l47	[ref]	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina submuralis</i>	l50	[ref]	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina uniseptata</i>	l41	100	<i>Aulaxinella</i>	<i>Aulaxinella</i>
<i>Aulaxina unispora</i>	l45	100	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Bullatina aspidota</i>	l75	[ref]	<i>Bullatina</i>	<i>Bullatina</i>
<i>Calenia africana</i>	l86	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia applanata</i>	l90	100	<i>Actinoplaca</i>	[<i>Aplanocalenia</i>]
<i>Calenia areolata</i>	l79	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia bullatinoides</i>	l88	[ref]	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia depressa</i>	l96	[ref]	<i>Calenia-Echinoplaca</i> grade	<i>Calenia</i>
<i>Calenia dictyospora</i>	l76	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia echinoplacoides</i>	l86	99	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia echinoplacoides</i>	l73	1	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia flava</i>	l77	90	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia flava</i>	l97	5	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia flava</i>	l96	4	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia flava</i>	l79	1	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia fumosa</i>	l86	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia graphidea</i>	l84	[ref]	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia inconspicua</i>	l77	43	<i>Calenia-Echinoplaca</i> grade	<i>Aplanocalenia</i>
<i>Calenia inconspicua</i>	l16	32	<i>Monocalenia</i>	<i>Aplanocalenia</i>
<i>Calenia inconspicua</i>	l18	16	<i>Monocalenia</i>	<i>Aplanocalenia</i>
<i>Calenia inconspicua</i>	l90	9	<i>Actinoplaca</i>	<i>Aplanocalenia</i>
<i>Calenia leptocarpa</i>	l96	49	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia leptocarpa</i>	l77	40	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia leptocarpa</i>	l80	9	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia leptocarpa</i>	l98	2	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia lobulata</i>	l73	[ref]	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia lueckingii</i>	l82	[ref]	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia maculans</i>	l39	100	<i>Caleniella</i>	<i>Caleniella</i>
<i>Calenia microcarpa</i>	l58	100	<i>Gyalectidium</i>	<i>Gyalectidium</i>
<i>Calenia minuta</i>	l89	86	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia minuta</i>	l88	11	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia minuta</i>	l91	3	<i>Vezdamyces</i>	[<i>Calenia</i>]
<i>Calenia monospora</i>	l18	[ref]	<i>Monocalenia</i>	<i>Monocalenia</i>
<i>Calenia obtecta</i>	l76	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia philippinensis</i>	l79	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia phyllogena</i>	l97	[ref]	<i>Calenia-Echinoplaca</i> grade	<i>Calenia</i>
<i>Calenia pruinosa</i>	l73	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia rionigrensii</i>	l79	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia rolandiana</i>	l16	86	<i>Monocalenia</i>	<i>Monocalenia</i>
<i>Calenia rolandiana</i>	l28	14	unresolved	<i>Monocalenia</i>
<i>Calenia solorinoides</i>	l17	[ref]	<i>Pseudocalenia</i>	<i>Pseudocalenia</i>
<i>Calenia subdepressa</i>	l86	53	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia subdepressa</i>	l79	47	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia submuralis</i>	l79	[ref]	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia thelotremella</i>	l79	97	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia thelotremella</i>	l97	3	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia triseptata</i>	l39	[ref]	<i>Caleniella</i>	<i>Caleniella</i>
<i>Calenia viridis</i>	l18	100	<i>Monocalenia</i>	<i>Monocalenia</i>

Table 1. — Continuation.

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

Table 1. — Continuation.

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

Table 1. — Continuation.

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

Table 1. — Continuation.

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

Table 1. — Continuation.

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

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.

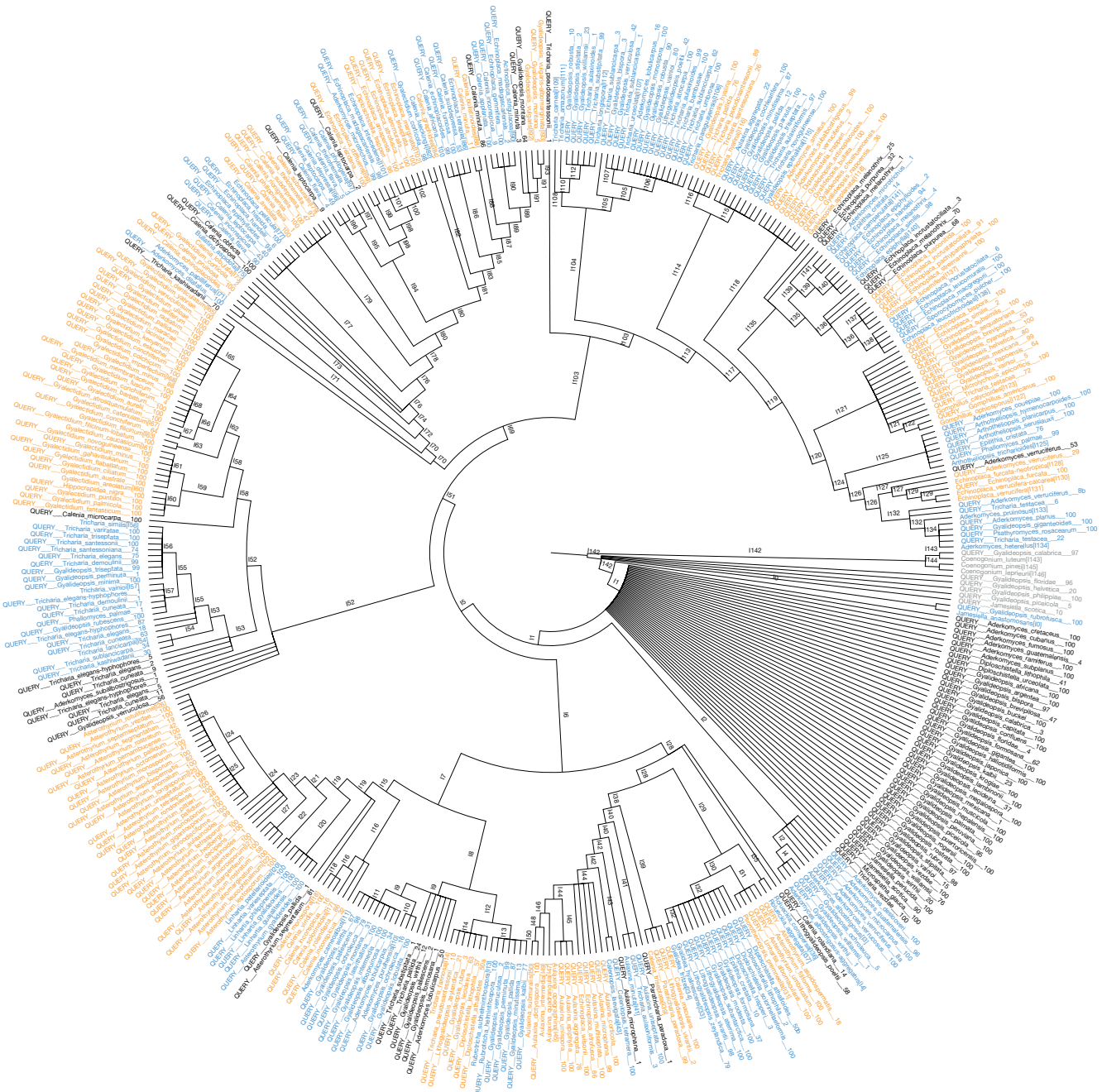


FIG. 2. — Result of the phenotype-based phylogenetic binning using taxa in the molecular reference and taxa based on their phenotype characters. The analysis includes node numbers on each branch and bootstrap support values from the binning approach for each query taxon after the query name. For full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

Acknowledgements

The Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) is thanked for a PhD scholarship to ABXL. The Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) is thanked for supporting the work abroad at the Botanical Garden and Botanical Museum Berlin Berlin (Processo 207282/2015-3), for funding the collecting trips (Processo 401186/2014-8), and for supporting a collaborative project with RL as Special Visiting Professor (Processo 314570/2014-4), as well as for the research grants to MESC (Processo 309058/2015-5) and BTG (300982/2016-3). This article is part of the PhD thesis of Amanda Barreto Xavier-Leite.

REFERENCES

- AHRENDT S. R., QUANDT C. A., CIOBANU D., CLUM A., SALAMOV A., ANDREPOULOS B., CHENG J. F., WOYKE T., PELIN A., HENRISSAT B., REYNOLDS N. K., BENNY G. L., SMITH M. E., JAMES T. Y. & GRIGORIEV I. V. 2018. — Leveraging single-cell genomics to expand the fungal tree of life. *Nature Microbiology* 3: 1417-1428. <https://doi.org/10.1038/s41564-018-0261-0>
- APTROOT A. & LÜCKING R. 2002. — Proposal to conserve *Gyalidea* (lichenized fungi: Asterothyriaceae, Ostropales) against an additional name, *Solorinella*. *Taxon* 51: 65. <https://doi.org/10.2307/1554877>
- BERGER S. A., KROMPASS D. & STAMATAKIS A. 2011a. — Performance, accuracy and web-server for evolutionary placement of short sequence reads under maximum-likelihood. *Systematic Biology* 60: 291-302. <https://doi.org/10.1093/sysbio/syr010>
- BERGER S. A., STAMATAKIS A. & LÜCKING R. 2011b. — Morphology-based phylogenetic binning of the lichen genera *Allographa* and *Graphis* (Ascomycota: Graphidaceae) using molecular site weight calibration. *Taxon* 60:1450-1457. <https://doi.org/10.1002/tax.605020>
- DAL-FORNO M., LÜCKING R., BUNGARTZ F., YÁNEZ-AYABACA A., MARCELLI M. P., SPELMANN A. A., COCA L. F., CHAVES J. L., APTROOT A., SIPMAN H. J. M., SIKAROODI M., GILLET M. & LAWREY J. D. 2016. — From one to six: unrecognized species diversity in the genus *Acantholichen* (lichenized Basidiomycota: Hygrophoraceae). *Mycologia* 108 (1): 38-55. <https://doi.org/10.3852/15-060>
- DIEDERICH P., LAWREY J. D. & ERTZ D. 2018. — The 2018 classification and checklist of lichenicolous fungi, with 2000 non-lichenized, obligately lichenicolous taxa. *The Bryologist* 121 (3): 340-425. <https://doi.org/10.1639/0007-2745-121.3.340>
- DOHRMANN M., KELLEY C., KELLY M., PISERA A., HOOPER J. N. & REISWIG H. M. 2017. — An integrative systematic framework helps to reconstruct skeletal evolution of glass sponges (Porifera, Hexactinellida). *Frontiers in Zoology* 14 (1): 18. <https://doi.org/10.1186/s12983-017-0191-3>
- ETAYO J. 2017. — Hongos Liquenícolas de Ecuador. *Opera Lilloana* 50: 1-535.
- FANG H., OATES M. E., PETHICA R. B., GREENWOOD J. M., SARDAR A. J., RACKHAM O. J., DONOGHUE P. C., STAMATAKIS A., DE LIMA MORAIS D. A. & GOUGH J. 2013. — A daily-updated tree of (sequenced) life as a reference for genome research. *Scientific Reports* 3: 2015. <https://doi.org/10.1038/srep02015>
- FERRARO L. I., LÜCKING R. & SÉRUSIAUX E. 2001. — A world monograph of the lichen genus *Gyalectidium* (Gomphillaceae). *Botanical Journal of the Linnean Society* 137 (3): 311-345. <https://doi.org/10.1111/j.1095-8339.2001.tb01126.x>
- GALINDO L. J., LÓPEZ-GARCÍA P., TORRUELLA G., KARPOV S. & MOREIRA D. 2021. — Phylogenomics of a new fungal phylum reveals multiple waves of reductive evolution across *Holomycota*. *Nature Communications* 12 (1): 4973. <https://doi.org/10.1038/s41467-021-25308-w>
- GRUBE M., BALOCH E. & LUMBSCH H. T. 2004. — The phylogeny of Porinaceae (Ostropomycetidae) suggests a neotenic origin of perithecia in Lecanoromycetes. *Mycological Research* 108: 1111-1118. <https://doi.org/10.1017/S0953756204000826>
- GUTTERES D. C., DOS SANTOS M. D. M., DA SILVA R. A. F., SOUZA E. S. C., SOARES W. R. O., PINHO D. B. & DIANESE J. C. 2020. — *Cladosterigma*: an enigmatic fungus, previously considered a basidiomycete, now revealed as an ascomycete member of the Gomphillaceae. *Mycologia* 112: 829-846. <https://doi.org/10.1080/00275514.2020.1781501>
- HENSSEN A. & LÜCKING R. 2002. — Morphology, anatomy, and ontogeny in the Asterothyriaceae (Ascomycetes: Ostropales), a greatly misunderstood group of lichenized fungi. *Annales Botanici Fennici* 39: 273-299.
- HERRERA-CAMPOS M. A., BARCENAS-PEÑA A., MIRANDA-GONZÁLEZ R., MEJÍA M. A., GONZÁLEZ J. A. B., COLÍN P. M., TÉLLEZ N. S. & LÜCKING R. 2019. — New lichenized Arthoniales and Ostropales from Mexican seasonally dry tropical forest. *The Bryologist* 122: 62-83. <https://doi.org/10.1639/0007-2745-122.1.062>
- HIBBETT D. S., BINDER M., BISCHOFF J. F., BLACKWELL M., CANNON P. F., ERIKSSON O. E., HUHNDOERF S., JAMES T., KIRK P. M., LÜCKING R., LUMBSCH H. T., LUTZONI F., MATHENY P. B., MC LAUGHLIN D. J., POWELL M. J., REDHEAD S., SCHOCH C. L., SPATAFORA J. W., STALPERS J. A., VILGALYS R., AIME M. C., APTROOT A., BAUER R., BEGEROW D., BENNY G. L., CASTLEBURY L. A., CROUS P. W., DAI Y. C., GAMS W., GEISER D. M., GRIFFITH G. W., GUEIDAN C., HAWKSWORTH D. L., HESTMARK G., HOSAKA K., HUMBER R. A., HYDE K. D., IRONSIDE J. E., KOLJALG U., KURTZMAN C. P., LARSSON K. H., LICHTWARDT R., LONGCORE J., MIADLIKOWSKA J., MILLER A., MONCALVO J. M., MOZLEY-STANDRIDGE S., OBERWINKLER F., PARMASO E., REEB V., ROGERS J. D., ROUX C., RYVARDEN L., SAMPAIO J. P., SCHUSSLER A., SUGIYAMA J., THORN R. G., TIBELL L., UNTEREINER W. A., WALKER C., WANG Z., WEIR A., WEISS M., WHITE M. M., WINKA K., YAO Y. J. & ZHANG N. 2007. — A higher-level phylogenetic classification of the Fungi. *Mycological Research* 111: 509-547. <https://doi.org/10.1016/j.mycres.2007.03.004>
- JAMES T. Y., KAUFF F., SCHOCH C. L., MATHENY P. B., HOFSTETTER V., COX C. J., CELIO G., GUEIDAN C., FRAKER E., MIADLIKOWSKA J., LUMBSCH H. T., RAUHUT A., REEB V., ARNOLD A. E., AMTOFT A., STAJICH J. E., HOSAKA K., SUNG G. H., JOHNSON D., O'ROURKE B., CROCKETT M., BINDER M., CURTIS J. M., SLOT J. C., WANG Z., WILSON A. W., SCHUSSLER A., LONGCORE J. E., O'DONNELL K., MOZLEY-STANDRIDGE S., PORTER D., LETCHER P. M., POWELL M. J., TAYLOR J. W., WHITE M. M., GRIFFITH G. W., DAVIES D. R., HUMBER R. A., MORTON J. B., SUGIYAMA J., ROSSMAN A. Y., ROGERS J. D., PFISTER D. H., HEWITT D., HANSEN K., HAMBLETON S., SHOEMAKER R. A., KOHLMAYER J., VOLKMAN-KOHLMEYER B., SPOTTS R. A., SERDANI M., CROUS P. W., HUGHES K. W., MATSUURA K., LANGER E., LANGER G., UNTEREINER W. A., LÜCKING R., BUDEL B., GEISER D. M., APTROOT A., DIEDERICH P., SCHMITT L.

- SCHULTZ M., YAHR R., HIBBETT D. S., LUTZONI F., MC LAUGHLIN D. J., SPATAFORA J. W. & VILGALYS R. 2006. — Reconstructing the early evolution of Fungi using a six-gene phylogeny. *Nature* 443: 818–822. <https://doi.org/10.1038/nature05110>
- KALB K. & VÉZDA A. 1988. — Neue oder bemerkenswerte Arten der Flechtenfamilie Gomphillaceae in der Neotropis. *Bibliotheca Lichenologica* 29: 1–80.
- KOCH M. A., KIEFER M., GERMAN D. A., AL-SHEHBAZ I. A., FRANZKE A., MUMMENHOFF K. & SCHMICKL R. 2012. — BrassiBase: Tools and biological resources to study characters and traits in the Brassicaceae – version 1.1. *Taxon* 61 (5): 1001–1009. <https://doi.org/10.1002/tax.615007>
- KRUG A. Z., JABLONSKI D. & VALENTINE J. W. 2008. — Species-genus ratios reflect a global history of diversification and range expansion in marine bivalves. *Proceedings of the Royal Society B* 275: 1117–1123. <https://doi.org/10.1098/rspb.2007.1729>
- LENAT D. R. & RESH V. H. 2001. — Taxonomy and stream ecology – The benefits of genus- and species-level identifications. *Journal of the North American Benthological Society* 20 (2): 287–298.
- LENDEMER J. C. 2017. — Revision of *Gyalideopsis ozarkensis* and *G. subaequatoriana* (Gomphillaceae; lichenized Ascomycetes), leads to the description of an overlooked new species. *The Bryologist* 120: 274–286. <https://doi.org/10.1639/0007-2745-120.3.274>
- LÜCKING R. 1997. — Estado actual de las investigaciones sobre líquenes foliícolas en la región Neotrópica, con un análisis biogeográfico preliminar. *Tropical Bryology* 13: 87–114.
- LÜCKING R. 1999. — Adiciones y correcciones al conocimiento de la líquenoflora foliícola de Costa Rica. La familia Asterothyriaceae y el género *Chroodiscus* (Thelotremaaceae), con un análisis filogenético. *Cryptogamie, Mycologie* 20: 193–224.
- LÜCKING R. 2008. — Follicolous Lichenized Fungi. *Flora Neotropica Monograph* 103: 1–866.
- LÜCKING R. 2019. — Stop the abuse of time! A critical review of temporal banding for rank-based classifications in Fungi (including lichens) and other organisms. *Critical Review in Plant Sciences* 38: 199–253. <https://doi.org/10.1080/07352689.2019.1650517>
- LÜCKING R. & KALB K. 2018. — Formal instatement of *Allographa* (Graphidaceae): how to deal with a hyperdiverse genus complex with cryptic differentiation and paucity of molecular data. *Herzogia* 31: 535–561. <https://doi.org/10.13158/heaia.31.1.2018.535>
- LÜCKING R., STUART B. & LUMBSCH H. T. 2004. — Phylogenetic relationships of Gomphillaceae and Asterothyriaceae – evidence from a combined Bayesian analysis of nuclear and mitochondrial sequences. *Mycologia* 96: 283–294. <https://doi.org/10.2307/3762064>
- LÜCKING R., SÉRUSIAUX E. & VÉZDA A. 2005. — Phylogeny and systematics of the lichen family Gomphillaceae (Ostropales) inferred from cladistic analysis of phenotype data. *The Lichenologist* 37 (2): 123–170. <https://doi.org/10.1017/S0024282905014660>
- LÜCKING R., BUCK W. R. & RIVAS PLATA E. 2007. — The lichen family Gomphillaceae (Ostropales) in eastern North America, with notes on hyphophore development in *Gomphillus* and *Gyalideopsis*. *The Bryologist* 110: 622–672. [https://doi.org/10.1639/0007-2745\(2007\)110\[622:TLFGOI\]2.0.CO;2](https://doi.org/10.1639/0007-2745(2007)110[622:TLFGOI]2.0.CO;2)
- LÜCKING R., ARCHER A. W. & APTROOT A. 2009. — A world-wide key to the genus *Graphis* (Ostropales: Graphidaceae). *The Lichenologist* 41: 363–452. <https://doi.org/10.1017/S0024282909008305>
- LÜCKING R., JOHNSTON M. K., APTROOT A., KRAICHAK E., LENDEMER J. C., BOONPRAGOB K., CÁCERES M. E. S., ERTZ D., FERRARO L. I., JIA Z.-F., KALB K., MANGOLD A., MANOCH L., MERCADO-DÍAZ J. A., MONCADA B., MONGKOLSUK P., PAPONG K., PARNMEN S., PELÁEZ R. N., POENGUNGNOEN V., RIVAS PLATA E., SAIPUNKAEW W., SIPMAN H. J. M., SUTJARITTURAKAN J., VAN DEN BROECK D., VON KONRAT M., WEERAKOON G. & LUMBSCH H. T. 2014. — One hundred and seventy-five new species of Graphidaceae: closing the gap or a drop in the bucket? *Phytotaxa* 189: 7–38. <https://doi.org/10.11646/phytotaxa.189.1.4>
- LÜCKING R., MANGOLD A., RIVAS PLATA E., PARNMEN S., KRAICHAK E. & LUMBSCH H. T. 2015. — Morphology-based phylogenetic binning to assess a taxonomic challenge: a case study in Graphidaceae (Ascomycota) requires a new generic name for the widespread *Leptotrema wightii*. *Botanical Journal of the Linnean Society* 179 (3): 436–443. <https://doi.org/10.1111/boj.12327>
- LÜCKING R., HODKINSON B. P. & LEAVITT S. D. 2017. — The 2016 classification of lichenized fungi in the Ascomycota and Basidiomycota – Approaching one thousand genera. *The Bryologist* 119: 361–416. <https://doi.org/10.1639/0007-2745-119.4.361>
- LÜCKING R., MONCADA B. & DAL FORNO M. 2023. — PhyloKey: a novel method to rapidly and reliably identify species in complex, species-rich genera, and an opportunity for ‘non-molecular museumics’. *The Lichenologist* 55 (5): 181–192. <https://doi.org/10.1017/S0024282923000415>
- LUTZONI F., KAUFF F., COX C., MC LAUGHLIN D., CELIO G., DENTINGER B., PADAMSEE M., HIBBETT D., JAMES T. Y., BALOCH E., GRUBE M., REEB V., HOFSTETTER V., SCHOCH C., ARNOLD A. E., MIADLIKOWSKA J., SPATAFORA J., JOHNSON D., HAMBLETON S., CROCKETT M., SHOEMAKER R., SUNG G.-H., LÜCKING R., LUMBSCH H. T., O’ DONNELL K., BINDER M., DIEDERICH P., ERTZ D., GUEIDAN C., HANSEN K., HARRIS R. C., HOSAKA K., LIM Y. W., MATHENY B., NISHIDA H., PFISTER D., ROGERS J., ROSSMAN A., SCHMITT I., SIPMAN H., STONE J., SUGIYAMA J., YAHR R. & VILGALYS R. 2004. — Assembling the fungal tree of life: Progress, classification, and evolution of subcellular traits. *American Journal of Botany* 91: 1446–1480. <https://doi.org/10.3732/ajb.91.10.1446>
- MC LAUGHLIN D. J., HIBBETT D. S., LUTZONI F., SPATAFORA J. W. & VILGALYS R. 2009. — The search for the fungal tree of life. *Trends in Microbiology* 17: 488–497. <https://doi.org/10.1016/j.tim.2009.08.001>
- MENEZES A. A., XAVIER-LEITE A. B., APTROOT A. & CÁCERES M. E. S. 2013. — New lichen species from the Caatinga in Chapada do Araripe, northeastern Brazil. *The Bryologist* 116 (3): 302–305.
- MIRANDA-GONZÁLEZ R., LÜCKING R., BARCENAS-PEÑA A. & HERRERA-CAMPOS M. A. 2020. — The new genus *Jocatoa* (Lecanoromycetes: Graphidaceae) and new insights into subfamily Redonographoideae. *The Bryologist* 123: 127–143. <https://doi.org/10.1639/0007-2745-123.2.127>
- MONCADA B., LÜCKING R. & SUÁREZ A. 2014. — Molecular phylogeny of the genus *Sticta* (lichenized Ascomycota: Lobariaceae) in Colombia. *Fungal Diversity* 64: 205–231. <https://doi.org/10.1017/S0024282912000825>
- PARNMEN S., LÜCKING R. & LUMBSCH H. T. 2012. — Phylogenetic classification at generic level in the absence of distinct phylogenetic patterns of phenotypic variation: a case study in Graphidaceae (Ascomycota). *PLoS ONE* 7: 1–13. <https://doi.org/10.1371/journal.pone.0051392>
- PERLMUTTER G. B., RIVAS PLATA E., LA GRECA S., APTROOT A., LÜCKING R., TEHLER A. & ERTZ D. 2020. — *Biatora akompsa* is revealed as a disjunct North American species of *Pentagenella* (Opogonaceae) through molecular phylogenetic analysis and phenotype-based binning. *The Bryologist* 123: 502–516. <https://doi.org/10.1639/0007-2745-123.3.502>
- RESH V. H. & MCELRAVY E. P. 1993. — Contemporary quantitative approaches to biomonitoring using benthic macroinvertebrates, in ROSENBERG D. M. & RESH V. H. (eds), *Fresh-Water Biomonitoring and Benthic Macroinvertebrates*. Chapman and Hall, New York: 159–194.
- RIVAS PLATA E., HERNÁNDEZ J. E., LÜCKING R., STAIGER B., KALB K. & CÁCERES M. E. S. 2011. — *Graphis* is two genera – A remarkable case of parallel evolution in lichenized Ascomycota. *Taxon* 60: 99–107.
- RIVAS PLATA E., LÜCKING R. & LUMBSCH H. T. 2012a. — A new classification for the Family Graphidaceae s. lat. (Ascomycota: Lecanoromycetes: Ostropales). *Fungal Diversity* 52: 107–121. <https://doi.org/10.1007/s13225-011-0135-8>

- RIVAS PLATA E., LÜCKING R. & LUMBSCH H. T. 2012b. — Molecular phylogeny and systematics of the *Ocellularia* clade (Ascomycota: Ostropales: Graphidaceae). *Taxon* 61: 1161-1179. <https://doi.org/10.1002/tax.616001>
- RIVAS PLATA E., PARNMEN S., STAIGER B., MANGOLD A., FRISCH A., WEERAKOON J., HERNÁNDEZ M. J. E., CÁCERES M. E. S., KALB K., SIPMAN H. J. M., COMMON R. S., NELSEN M. P., LÜCKING R. & LUMBSCH H. T. 2013. — A molecular phylogeny of Graphidaceae (Ascomycota: Lecanoromycetes: Ostropales) including 428 species. *MycKeys* 6: 55-94. <https://doi.org/10.3897/mycokeys.6.3482>
- ROUX C., PINAULT P. & ERTZ D. 2022. — *Corticifraga ramalinae* P. Pinault, Ertz et Cl. Roux sp. nov., champignon lichénicole non lichénisé (Ascomycota, Gomphillaceae). *Bulletin de la Société linnéenne de Provence* 73: 29-35.
- SPATAFORA J. W., CHANG Y., BENNY G. L., LAZARUS K., SMITH M. E., BERBEE M. L., BONITO G., CORRADI N., GRIGORIEV I., GRYGANSKYI A. & JAMES T. Y. 2016. — A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. *Mycologia* 108: 1028-1046. <https://doi.org/10.3852/16-042>
- SPRINGER M. S., SIGNORE A. V., PAIJMANS J. L. A., VÉLEZ-JUARBE J., DOMNING D. P., BAUER C. E., HE K., CRERAR L., CAMPOS P. F., MURPHY W. J., MEREDITH R. W., GATESY J., WILLERSLEV E., MACPHEE R. D. E., HOFREITER M. & CAMPBELL K. L. 2015. — Interordinal gene capture, the phylogenetic position of Steller's sea cow based on molecular and morphological data, and the macroevolutionary history of *Sirenia*. *Molecular Phylogenetics and Evolution* 91: 178-193. <https://doi.org/10.1016/j.ympev.2015.05.022>
- STAMATAKIS A. 2006. — RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22 (21): 2688-2690. <https://doi.org/10.1093/bioinformatics/btl446>
- STAMATAKIS A. 2014. — RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30 (9): 1312-1313. <https://doi.org/10.1093/bioinformatics/btu033>
- STAMATAKIS A., LUDWIG T. & MEIER H. 2005. — RAxML-III: a fast program for maximum likelihood-based inference of large phylogenetic trees. *Bioinformatics* 21 (4): 456-463. <https://doi.org/10.1093/bioinformatics/bti191>
- STAMATAKIS A., HOOVER P. & ROUGEMONT J. 2008. — A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology* 57 (5): 758-771. <https://doi.org/10.1080/10635150802429642>
- TEDERSOO L., SÁNCHEZ-RAMÍREZ S., KOLJALG U., BAHRAM M., DÖRING M., SCHIGEL D., MAY T., RYBERG M. & ABARENKOV K. 2018. — High-level classification of the Fungi and a tool for evolutionary ecological analyses. *Fungal Diversity* 90: 135-159. <https://doi.org/10.1007/s13225-018-0401-0>
- TESTO W., OLLGAARD B., FIELD A., ALMEIDA T., KESSLER M. & BARRINGTON D. 2018. — Phylogenetic systematics, morphological evolution, and natural groups in neotropical *Phlegmariurus* (Lycopodiaceae). *Molecular Phylogenetics and Evolution* 125: 1-13. <https://doi.org/10.1016/j.ympev.2018.03.016>
- VÉZDA A. 1973. — Foliicole Flechten aus der Republik Guinea (W. Afrika). I. *Acta Musei Silesiae, Opava* 22: 67-90.
- VÉZDA A. & POELT J. 1987. — Flechtensystematische Studien. XII. Die Familie Gomphillaceae und ihre Gliederung. *Folia Geobotanica et Phytotaxonomica, Praha* 22: 179-198.
- WIJAYAWARDENE N. N., HYDE K. D., DAI D. Q., SÁNCHEZ-GARCÍA M., GOTO B. T., SAXENA R. K., ERDOĞDU M., SELÇUK F., RAJESHKUMAR K. C., APTROOT A., BŁASZKOWSKI J., BOONYUEN N., DA SILVA G. A., DE SOUZA F. A., DONG W., ERTZ D., HAELEWATERS D., JONES E. B. G., KARUNARATHNA S. C., KIRK P. M., KUKWA M., KUMLA J., LEONTYEV D. V., LUMBSCH H. T., MAHARACHCHIKUMBURA S. S. N., MARGUNO F., MARTÍNEZ-RODRÍGUEZ P., MEŠIĆ A., MONTEIRO J. S., OEHL F., PAWŁOWSKA J., PEM D., PFLIEGLER W. P., PHILLIPS A. J. L., POŠTA A., HE M. Q., LI J. X., RAZA M., SRUTHI O. P., SUETRONG S., SUWANNARACH N., TEDERSOO L., THIYAGARAJA V., TIBPROMMA S., TKALČEC Z., TOKAREV Y. S., WANASINGHE D. N., WIJESUNDARA D. S. A., WIMALASEANA S. D. M. K., MADRID H., ZHANG G. Q., GAO Y., SÁNCHEZ-CASTRO I., TANG L. Z., STADLER M., YURKOV A. & THINES M. 2022. — Outline of Fungi and fungus-like taxa – 2021. *Mycosphere* 13: 53-453. <https://doi.org/10.5943/mycosphere/13/1/2>
- XAVIER-LEITE A. B., CÁCERES M. E. S., GOTO B. T. & LÜCKING R. 2018. — The genus *Gyalideopsis* (lichenized Ascomycota: Gomphillaceae) in Brazil: updated checklist, key to species, and two novel taxa with unique hyphophores. *The Bryologist* 121 (1): 32-40. <https://doi.org/10.1639/0007-2745-121.1.032>
- XAVIER-LEITE A. B., CÁCERES M. E. S., APTROOT A. MONCADA B., LÜCKING R. & GOTO B. T. 2022. — Phylogenetic revision of the lichenized family Gomphillaceae (Ascomycota: Graphidales) suggests post-K–Pg boundary diversification and phylogenetic signal in asexual reproductive structures. *Molecular Phylogenetics and Evolution* 168: 107380. <https://doi.org/10.1016/j.ympev.2021.107380>
- XAVIER-LEITE A. B., GOTO B. T., LÜCKING R. & CÁCERES M. E. S. 2023. — New genera in the lichenized family Gomphillaceae (Ascomycota: Graphidales) focusing on neotropical taxa. *Mycological Progress* 22: 88. <https://doi.org/10.1007/s11557-023-01933-1>

Submitted on 10 July 2023;
accepted on 21 December 2023;
published on 9 August 2024.

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