



UNIVERSIDADE FEDERAL DO RIO GRANDE DO NORTE
CENTRO DE BIOCÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM SISTEMÁTICA E EVOLUÇÃO

REVISÃO DA FAMÍLIA GOMPHILLACEAE (ASCOMYCOTA
LIQUENIZADO): FILOGENIA, SISTEMÁTICA E EVOLUÇÃO

AMANDA BARRETO XAVIER LEITE

Tese de Doutorado
Natal/RN, agosto de 2018

AMANDA BARRETO XAVIER LEITE

**REVISÃO DA FAMÍLIA GOMPHILLACEAE (ASCOMYCOTA
LIQUENIZADO): FILOGENIA, SISTEMÁTICA E EVOLUÇÃO**

Tese de doutorado apresentada
ao Programa de Pós-Graduação
em Sistemática e Evolução da
Universidade Federal do Rio
Grande do Norte, em
cumprimento às exigências para
a obtenção do título de Doutor
em Sistemática e Evolução

Área de concentração: taxonomia e sistemática

Orientador: Dr. Bruno Tomio Goto

Coorientadora: Dra. Marcela Eugenia da Silva Cáceres

Coorientador: Dr. Robert Karl Lücking

Natal - RN

2018

Universidade Federal do Rio Grande do Norte - UFRN
Sistema de Bibliotecas - SISBI

Catálogo de Publicação na Fonte. UFRN - Biblioteca Setorial Prof. Leopoldo Nelson - -Centro de Biociências - CB

Leite, Amanda Barreto Xavier.

Revisão da família GOMPHILLACEAE (ASCOMYCOTA LIQUENIZADO):
filogenia, sistemática e evolução / Amanda Barreto Xavier Leite.
- Natal, 2018.
253 f.: il.

Tese (Doutorado) - Universidade Federal do Rio Grande do
Norte. Centro de Biociências. Programa de Pós-Graduação em
Sistemática e Evolução.

Orientador: Dr. Bruno Tomio Goto.

Coorientadora: Dra. Marcela Eugenia da Silva Cáceres.

Coorientador: Dr. Robert Karl Lücking.

1. Filogenia - Tese. 2. Foliícolas - Tese. 3. Nomenclatura -
Tese. I. GOTO, Bruno Tomio et al. II. Título.

RN/UF/BSE-CB

CDU 575.8

AMANDA BARRETO XAVIER LEITE

**REVISÃO DA FAMÍLIA GOMPHILLACEAE (ASCOMYCOTA LIQUENIZADO):
FILOGENIA, SISTEMÁTICA E EVOLUÇÃO**

Tese apresentada ao Programa de Pós-graduação em Sistemática e Evolução da Universidade Federal do Rio Grande do Norte como requisito parcial para obtenção do título de Doutora em Sistemática e Evolução.

Aprovada em 31 de agosto de 2018.

Comissão examinadora

Dra. Eugênia Cristina Gonçalves Pereira, UFPE
Examinador Externo à Instituição

Dr. José Luiz Bezerra, UFRB
Examinador Externo à Instituição

Dra. Manuela Dal Forno, SNMNH
Examinador Externo à Instituição

Dra. Raquel Cordeiro Theodoro, UFRN
Examinador Interno

Dr. Bruno Tomio Goto, UFRN
Presidente

Dedico ao meu pai e
minha mãe, Crisóstomo
Pereira Leite e Mirsa Mara
B. X. Leite, e ao meu
amor, Rodrigo Gonçalves
Meneses, pela caminhada
juntos.

AGRADECIMENTOS

Meus agradecimentos iniciais vão para a Universidade Federal do Rio Grande do Norte e ao Programa de Pós-Graduação em Sistemática e Evolução pela oportunidade de conhecer e cursar o Doutorado, bem como ao Botanischer Garden und Botanisches Museum (BGBM) por me receber e fornecer estrutura e material para as análises moleculares e morfológicas da pesquisa.

À Coordenação de Aperfeiçoamento de Pessoa de Nível Superior (CAPES) pelo apoio financeiro através da bolsa de Doutorado e ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) pelo suporte financeiro na pesquisa através do Projeto Universal (Processo 401186/2014-8) e o Projeto Professor Visitante Especial (Processo 314570/2014-4), que me proporcionaram desenvolver o Doutorado sanduíche em Berlim, Alemanha.

Ao Prof. Dr. Bruno Tomio Goto por me receber na UFRN e no Laboratório de Biologia de Micorrizas (LBM) com tanto carinho e atenção. Nesses quatro anos tive o prazer de trabalhar e aprender muito com um profissional tão dedicado e amigo. Obrigada também pela confiança e incentivo na vida acadêmica e pessoal, além das cobranças sempre valiosas.

À Profa. Dra. Marcela Cáceres, que de orientadora e mãe científica se tornou uma grande amiga que admiro cada vez mais. Gratidão por tanto que tem feito por mim desde a monitoria até o Doutorado (e já se foram 10 anos!), mas, com certeza, foram nesses últimos quatro anos que pudemos crescer e amadurecer nossa relação que vai além dos líquens. E, um obrigada especial a sua sensibilidade e cuidado no momento que mais precisei durante o Doutorado.

Ao Dr. Robert Lücking por toda atenção e dedicação durante tantos anos de pesquisa. É uma honra poder aprender, conviver e trabalhar com um pesquisador que tanto admiro. E obrigada por ter me recebido em Berlim para o Doutorado sanduíche auxiliando e ensinando sobre a família Gomphillaceae com tanta paciência e maestria. E, claro, por ter me apresentado o currywurst.

Aos queridos Professores e Professoras que aceitaram fazer parte da banca: Dra. Eugênia Pereira, Dra. Manuela Dal Forno, Dra. Raquel Theodoro, Dr. José Luiz Bezerra, Dr. Iuri Baseia e Dr. Roger Melo. Obrigada!

Ao querido e grande liquenólogo, Dr. Harrie Sipman, pelos ensinamentos, pelas conversas enriquecedoras e pelo carinho durante minha estadia em Berlin. Muito obrigada, foi uma satisfação imensa poder conhecê-lo.

Aos queridos Dra. Bibiana Moncada e Msc. Dubán Canal por todo auxílio prestado no Laboratório do BGBM durante as análises moleculares e por tantos momentos de descontração em Berlim. Sem a ajuda de vocês, tantas espécies não teriam sido sequenciadas e o estudo da família não seria tão completo. Muito obrigada.

Um agradecimento especial à minha grande amiga que Berlim me deu, Nana Silakdze. Obrigada por ter me acolhido em sua casa, por ter tornado os dias difíceis em alegres e ter amenizado a saudade da família e amigos com seu carinho fraternal.

Às amigas que o LBM me presenteou, Khadija Jobim, Flor e Stephania. Obrigada, meninas, por tanto carinho, alegria e aprendizado. Além das trocas acadêmicas e pessoais valiosas que nossos cafés com avelã renderam, serei eternamente grata pela recepção e amizade conquistada.

Ao casal querido, Dônis e Pâmela, pela amizade e pelos cuidados enquanto estive em Natal, principalmente.

À minha fisioterapeuta, Tathiany Moura, e ao meu ortopedista, Dr. João Bourbon, que se tornaram amigos. Dois grandes profissionais que tive a sorte e honra de ter conhecido. Sem a dedicação e profissionalismo de vocês tudo teria sido muito mais difícil e doloroso. Serei eternamente grata e orgulhosa do trabalho lindo que fizeram comigo. Muito obrigada.

Às queridas sogra e cunhada, Dilma e Eldinha, pelo carinho, preocupação e atenção de sempre.

Aos queridos Pepita e João Liparoti pelo cuidado e companhia enquanto estive em Natal, como também à querida amiga Gilvanise e família pelo acolhimento e recepção sempre cheios de carinho.

Às minhas queridas cunhadas Tássia e Thábata pela amizade e carinho.

Aos grandes e eternos amigos que estiveram comigo nessa caminhada me apoiando, alegrando e incentivando, mesmo que nos momentos mais difíceis e nos quais estive ausente: Aline, Amanda, Amélia, Arthur, Brenda, Carol Lins, Carol Moura, David, Dora, Elaine, Janaína, Juliana, Larinha, Laura, Raquel, Tainah, Valéria e Verinha. Amo vocês.

À minha Avó, Mirian Barreto, por ser essa mulher tão especial e inspiradora em nossas vidas. E ao meu avô, Josemir Xavier, por todo carinho e atenção. Agradeço também à minha Tia Thatiane e Leni, sempre presentes e cheias de amor e carinho. E aos primos que me acolheram em Natal com tanto amor, Mytchel, Paulinha e, meu denço, Henry. Amo vocês.

Ao grande motivo de seguir em frente, os que mostram o caminho mais leve e carregam as dores comigo: minha família! Aos meus pais, Mirsa e Crisóstomo, meu eterno obrigado por tanto amor e incentivo. Aos meus irmãos, Erick e Vinicius, por alegrarem meus

dias e estarem sempre ao meu lado. Às minhas sobrinhas, que vieram para somar, unir e alegrar nossas vidas, Amorinha e Violetinha. E a Vaninha por tanto carinho e amor. Obrigada e amo muito vocês.

E um agradecimento especial ao meu companheiro de vida e de Doutorado, Rodrigo Meneses. Foram quatro anos de momentos bons e ruins, de muita distância, mas que foram sempre supridos com muita confiança, amor e companheirismo. A caminhada ao seu lado é sempre mais leve. Obrigada por tudo. Amo você.

Assim, é da guerra da natureza, da fome e da morte, que deriva diretamente o mais exaltado objeto que somos capazes de conceber, a produção de animais superiores. Há grandeza nessa visão da vida, com seus tantos poderes tendo sido originalmente insuflados em algumas poucas formas ou em apenas uma; e de que, enquanto este planeta girava seguindo a lei imutável da gravidade, de um começo tão simples, infinitas formas, as mais belas e as mais maravilhosas, evoluíram e continuam evoluindo. (Charles Darwin)

RESUMO

Dentre as famílias de líquens foliícolas, Gomphillaceae é considerada uma das mais diversas. O objetivo do trabalho é revisar a família Gomphillaceae (Ascomycota liquenizados), especialmente as espécies foliícolas, utilizando caracteres morfológicos e moleculares. A metodologia utilizada consistiu de amostras coletadas em áreas de Mata Atlântica, Brejo de Altitude e Amazônia, no Brasil, somadas a amostras coletadas em outros países da América Latina como Cuba, México, Panamá, Costa Rica e Guatemala. O material coletado foi prensado, refrigerado, analisado e selecionado de acordo com a presença de representantes da família Gomphillaceae. Após isso, as amostras foram identificadas, revisadas morfológicamente e analisadas molecularmente utilizando os marcadores mtSSU rDNA e nuLSU rDNA. Foram coletadas 2.127 folhas contendo líquens foliícolas e 502 espécimes foram selecionadas para identificação e análise molecular. Porém, 309 espécimes foram utilizados na análise filogenética final para a família, somadas a 28 do GenBank (incluindo o *outgroup*). Foi obtido um total de 464 sequências para a família Gomphillaceae, sendo 272 novas para nuLSU e 136 novas para mtSSU. Os resultados obtidos a partir deste trabalho servem para explicar a distribuição de gêneros e espécies pertencentes a Gomphillaceae, contribuindo para o conhecimento sistemático evolutivo já que são descritos 13 novos gêneros estabelecidos filogeneticamente para a família (*Adelphomyces* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Aptrootidea* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Aulaxinella* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Batistomyces* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Bezerroplaca* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Caleniella* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Monocalenia* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Pseudocalenia* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Roselviria* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Serusiauxiella* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Sipmanidea* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Verruciplaca* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, and *Veždomyces* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*), quatro gêneros restabelecidos (*Microxyphiomyces* Bat., Valle & Peres, *Psathyromyces* Bat. & Peres, *Spinomyces* Bat. & Peres ex Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, and *Sporocybomyces* H. Maia), e 53 novas combinações são introduzidas para as espécies incluídas nos gêneros novos e restabelecidos. Além disso, as análises confirmaram grupos polifiléticos, gêneros previamente distintos e bem suportados. Além disso, alguns pequenos gêneros ainda não foram amostrados molecularmente.

Palavras-chave: Foliícolas, filogenia, nomenclatura, rDNA

ABSTRACT

Gomphillaceae is considered one of the most diverse families of foliicolous lichens. The objective of the present research is to review the family Gomphillaceae (Ascomycota lichenized), especially the foliicolous taxa, using morphological and molecular characters. The methodology consisted of using samples collected in areas of Atlantic Forest, Brejo de Altitude and Amazon, in Brazil, in addition to samples collected in other Latin American countries such as Cuba, Mexico, Panama, Costa Rica and Guatemala. The collected material was pressed, refrigerated, analyzed and selected according to the presence of representatives of the family Gomphillaceae. After that, the samples were identified, morphologically reviewed and molecularly analyzed using the mtSSU rDNA and nuLSU rDNA markers. A total of 2,127 leaves containing foliicolous lichens was collected and 502 specimens were selected for identification and molecular analysis. However, 309 specimens were used in the final phylogenetic analysis for the family, added to 28 sequences from GenBank (including the outgroup). A total of 464 sequences were obtained for the Gomphillaceae family, 272 new for nuLSU and 136 new for mtSSU. The results obtained from this work help to explain the distribution of genera and species belonging to Gomphillaceae, contributing to the systematic evolutionary knowledge within the group. 13 new genera phylogenetically established for the family (*Adelphomyces* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Aptrootidea* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Aulaxinella* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Batistomyces* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Bezerroplaca* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Caleniella* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Monocalenia* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Pseudocalenia* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Roselviria* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Serusiauxiella* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Sipmanidea* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Verruciplaca* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, and *Veزدamyces* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*), four newly reinstated genera (*Microxyphiomyces* Bat., Valle & Peres, *Psathyromyces* Bat. & Peres, *Spinomyces* Bat. & Peres ex Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, and *Sporocybomyces* H. Maia), and 53 new combinations are introduced for species included in the new and re-established genera. In addition, the analyzes confirmed polyphyletic groups, and the previously distinguished and well supported genera. Finally, some small genera have not yet been molecularly sampled.

Keywords: Follicolous, phylogeny, nomenclature, rDNA

LISTA DE FIGURAS

- Figura 1:** Diferentes cores de setas presentes nos talos da família Gomphillaceae. **A–B.** Setas pretas comumente encontradas em talos de *Tricharia*. **C–D.** Representantes do gênero *Echinoplaca* e a presença de setas brancas. **E–F.** Talos de *Caleniopsis* e *Rubrotricha*, respectivamente, com setas vermelhas. **G–H.** Exemplos de gêneros que não possuem setas, como *Aulaxina* e *Asterothyrium*, respectivamente31
- Figura 2:** Hifóforos e esporos em espécies foliícolas da família Gomphillaceae. **A.** Estruturas microscópicas do hifóforo, pedúnculo e ápice, e as diahifas. **B.** Hifóforos *squamiform* de *Gyalectidium filicinum*. **C–D.** Hifóforos *flabellate* e esporo muriforme hialino pertencentes ao gênero *Aderkomyces*. **E.** Esporo muriforme e hialino do gênero *Tricharia*. **F.** Esporo transversalmente septado e hialino do gênero novo descrito no presente trabalho32
- Figura 3:** Diferentes tipos de apotécios encontrados na família Gomphillaceae. **A.** Apotécio erumpente carbonizado de *Aulaxina*. **B.** Apotécio sésstil de *Tricharia*. **C–D.** Apotécios *adnate* de *Echinoplaca*. **E–F.** Apotécios *applanate-sessile* pertencentes ao gênero *Gyalectidiopsis*. **G–H.** Apotécios *erumpent-zeorine* do gênero *Gyalectidium*33
- Figura 4:** Mapa do Brasil com pontos de coletas realizadas nas áreas de Mata Atlântica, Brejo de Altitude e Amazônia.....35
- Figura 5:** Áreas de coletas de líquens foliícolas da família Gomphillaceae representando o Brejo de Altitude. **A–D.** O Parque Estadual Mata do Pau-Ferro, localizado no estado da Paraíba, Nordeste, Brasil. **E–H.** A Serra da Jiboia, localizada no estado da Bahia, Nordeste, Brasil.....39
- Figura 6:** Áreas de coleta de representantes da família Gomphillaceae no Nordeste brasileiro e consideradas áreas de Brejo de Altitude, localizadas no Bioma Caatinga. **A–D.** O Parque Ecológico Municipal João Vasconcelos Sobrinho, mais conhecido por Brejo dos Cavalos, localiza-se no estado de Pernambuco, Brasil. **E–H.** A Serra da Guia, localizada no estado de Sergipe, mais precisamente no município de Poço Redondo40
- Figura 7:** Áreas de Mata Atlântica no Nordeste brasileiro, onde amostras de líquens foliícolas da família Gomphillaceae foram coletadas. **A–D.** Reserva Biológica Guaribas (Rebio Guaribas), localizado no estado da Paraíba. **E–H.** O Parque Nacional Serra de Itabaiana, localizado no estado de Sergipe.....41
- Figura 8:** Unidades de Conservação que representam áreas de Mata Atlântica em que coletas foram realizadas durante a pesquisa de líquens da família Gomphillaceae. **A–D.** Parque

Nacional do Itatiaia (PNI), localizado na região Sudeste do Brasil. **E–H.** Reserva Biológica de Uma (Rebio Una), localizado no estado da Bahia, Nordeste do Brasil.....42

Figura 9: Áreas de coletas de líquens foliícolas. **A–D.** A Estação Biológica Santa Lúcia, localiza-se no estado do Espírito Santo e representa a Mata Atlântica no Sudeste do Brasil. **E–H.** A Floresta Nacional do Amapá ou FLONA do Amapá, encontra-se no estado do Amapá, região Norte, e representa a Amazônia brasileira.....43

Figura 10: Análises morfológica e molecular dos espécimes selecionados no *BGBM*, Berlin, Alemanha. **A–B.** Fotos das etiquetas, folhas e espécimes selecionados. **C.** Sala devidamente estruturada para análise morfológica e microscópica. **D.** Confecção de etiquetas para análise molecular. **E–F.** Tubos de eppendorfs preparados para extração de DNA e amplificação por PCR. **G–H.** Eletroforese em gel de agarose e resultado das bandas dos produtos da PCR46

Capítulo 1:

Figure 1: Overall cartoon phylogeny of Gomphillaceae as inferred from a two gene concatenated, maximum-likelihood analysis of mtSSU and nuLSU rDNA data. Details including bootstrap support values are given in the corresponding figures (Fig. 2–4).77

Figure 2: Partial phylogeny of Gomphillaceae (best-scoring maximum likelihood tree) showing details in the basal portion of the tree. Bootstrap values are indicated below the branches. Alternating colors (blue versus black) indicating lineages recognized at genus level, and Labels indicate applicable, available, and newly suggested genus names as follows: grey = long established names; blue = more recently established names; red = names based on Batista and co-workers for hyphophore anamorphs; orange = newly proposed names.78

Figure 3: Partial phylogeny of Gomphillaceae (best-scoring maximum likelihood tree) showing details in the mid portion of the tree. Bootstrap values are indicated below the branches. Alternating colors (blue versus black) indicating lineages recognized at genus level, and Labels indicate applicable, available, and newly suggested genus names as follows: grey = long established names; blue = more recently established names; red = names based on Batista and co-workers for hyphophore anamorphs; orange = newly proposed names.79

Figure 4: Partial phylogeny of Gomphillaceae (best-scoring maximum likelihood tree) showing details in the apical portion of the tree. Bootstrap values are indicated below the branches. Alternating colors (blue versus black) indicating lineages recognized at genus level, and Labels indicate applicable, available, and newly suggested genus names as follows: grey = long established names; blue = more recently established names; red = names based on Batista and co-workers for hyphophore anamorphs; orange = newly proposed names.80

Capítulo 2:

Figure 1: New genus <i>Adelphomyces</i> , sequenced specimen. <i>Adelphomyces epithallinus</i> , Brazil [23107].	98
Figure 2: New genus <i>Aptrootidea</i> , including sequenced specimens. A. <i>Aptrootidea marginata</i> , Costa Rica. B. <i>A. marginata</i> , Brazil [23012]. C. <i>A. marginata</i> , Brazil [23114]. D. <i>A. marginata</i> , Brazil [23015]. E. <i>A. marginata</i> , Brazil [23013]. F. <i>Aptrootidea</i> sp. nov., Brazil [22024].	100
Figure 3: New genus <i>Aptrootidea</i> . A. <i>Aptrootidea amapensis</i> , Brazil. B. <i>A. atrofusca</i> . C. <i>A. atromuralis</i> , Costa Rica. D. <i>A. triseptata</i> , Costa Rica.	101
Figure 4: New genus <i>Aulaxinella</i> , including sequenced specimens. A. <i>Aulaxinella minuta</i> , Ecuador. B. <i>A. aff. minuta</i> , Brazil [23079]. C. <i>A. aff. minuta</i> , Brazil [23092]. D. <i>A. aff. minuta</i> , Brazil [22173]. E. <i>A. minuta</i> , Brazil [22186]. F. <i>A. minuta</i> , Brazil [22187].	103
Figure 5: New genus <i>Batistomyces</i> , including sequenced specimens. A. <i>Batistomyces hyalinus</i> , French Guiana. B. <i>B. hyalinus</i> , Brazil [23154]. C. <i>B. hyalinus</i> , Brazil [23155]. D. <i>B. pallidus</i> , holotype.	107
Figure 6: New genus <i>Bezerroplaca</i> . A. <i>Bezerroplaca lucernifera</i> , Ecuador. B. <i>B. lucernifera</i> , Costa Rica. C. <i>B. fusconitida</i> , Costa Rica. D. <i>B. incrustatociliata</i> , Papua New Guinea, E. <i>B. pachyparaphysata</i> , Brazil. F. <i>B. streimannii</i> , Australia.	108
Figure 7: New genus <i>Caleniella</i> and reinstated genus <i>Microxyphiomyces</i> , including sequenced specimens. A. <i>Caleniella triseptata</i> , Costa Rica. B. <i>C. triseptata</i> , Brazil [23146]. C. <i>Microxyphiomyces lancicarpus</i> , French Guiana. D. <i>M. lancicarpus</i> , Brazil [22164].	109
Figure 8: New genus <i>Microxyphiomyces</i> , including sequenced specimens. A. <i>Microxyphiomyces vainioi</i> , Costa Rica. B. <i>M. vainioi</i> , Brazil [22176]. C. <i>M. vainioi</i> , Brazil [22004]. D. <i>M. vainioi</i> , Brazil [23075]. E. <i>M. vainioi</i> , Brazil [23111]. F. <i>M. vainioi</i> , Brazil [23077].	112
Figure 9: Reinstated genus <i>Microxyphiomyces</i> , including sequenced specimens. A. <i>Microxyphiomyces demoulinii</i> , Papua New Guinea. B. <i>M. similis</i> , holotype. C. <i>M. similis</i> , Brazil [22147]. D. <i>M. variratae</i> , holotype.	113
Figure 10: New genus <i>Microxyphiomyces</i> . A. <i>Microxyphiomyces cuneatus</i> , Paraguay. B. <i>M. cuneatus</i> , holotype. C. <i>M. kashiwadani</i> , Japan. D. <i>M. santessoni</i> , holotype.	114
Figure 11: New genera <i>Monocalenia</i> and <i>Pseudocalenia</i> . A. <i>Monocalenia monospora</i> , Costa Rica. B. <i>M. monospora</i> , holotype. C. <i>Pseudocalenia solorinoides</i> , holotype. D. <i>Pseudocalenia</i> sp., Guatemala [22815].	116
Figure 12: Reinstated genus <i>Psathyromyces</i> , including sequenced specimens. A. <i>Psathyromyces heterellus</i> , Guyana. B. <i>P. heterellus</i> , Brazil [22028]. C. <i>P. heterellus</i> , Brazil	

[22097]. D. <i>P. heterellus</i> , Brazil [22130]. E. <i>P. aff. heterellus</i> , Brazil [23163]. F. <i>P. planus</i> (Vězda) Xavier-Leite, M. Cáceres & Lücking, holotype.	120
Figure 13: New genus <i>Roselviria</i> , including sequenced specimens. A. <i>Roselviria purulhensis</i> , Costa Rica. B. <i>R. purulhensis</i> , Brazil [22196]. C. <i>R. purulhensis</i> , Brazil [23104]. D. <i>R. lobulimarginata</i> , Malaysia (holotype).....	121
Figure 14: New genus <i>Serusiauxiella</i> , including sequenced specimens. A. <i>Serusiauxiella farinosa</i> , Brazil. B. <i>S. farinosa</i> , Brazil [23062]. C. <i>S. farinosa</i> , Brazil [23063]. D. <i>S. farinosa</i> , Brazil [23065]. E. <i>S. aff. farinosa</i> , Guatemala [22801]. F. <i>S. aff. farinosa</i> , Guatemala [22809]. ...	122
Figure 15: New genus <i>Sipmanidea</i> , including sequenced specimens. A. <i>Sipmanidea neotropica</i> , Ecuador. B. <i>S. neotropica</i> , Ecuador. C. <i>S. neotropica</i> , Brazil [23016]. D. <i>S. neotropica</i> , Brazil [23143]. E. <i>S. neotropica</i> , Brazil [23144]. F. <i>S. furcata</i> , holotype.....	127
Figure 16: Reinstated and validated genus <i>Spinomyces</i> , including sequenced specimens. A. <i>Spinomyces albostrigosus</i> , Costa Rica. B. <i>S. albostrigosus</i> , Brazil [22194]. C. <i>S. aggregatus</i> , Guatemala. D. <i>S. aggregatus</i> , Brazil [22195]. E. <i>S. deslooveri</i> , holotype. F. <i>S. guatemalensis</i> , Guatemala.....	128
Figure 17: Reinstated genus <i>Sporocybomyces</i> , including sequenced specimens. A. <i>Sporocybomyces leucotrichoides</i> , Costa Rica. B. <i>S. leucotrichoides</i> , Brazil [22046]. C. <i>S. leucotrichoides</i> , Brazil [22030]. D. <i>S. leucotrichoides</i> , Brazil [23008]. E. <i>S. leucotrichoides</i> , Brazil [22013]. F. <i>S. leucomuralis</i> , Brazil.....	129
Figure 18: New genus <i>Verruciplaca</i> , including sequenced specimens. A. <i>Verruciplaca verrucifera</i> , Costa Rica. B. <i>V. verrucifera</i> , Brazil [22069]. C. <i>V. verrucifera</i> , Brazil [22068]. D. <i>Verruciplaca</i> sp., Panama [22893]. E. <i>V. calcarea</i> , Costa Rica. F. <i>V. calcarea</i> , Brazil [22198].	133
Figure 19: New genus <i>Veždamyces</i> , including sequenced specimens. A. <i>Veždamyces vulgaris</i> , Costa Rica. B. <i>V. vulgaris</i> , Costa Rica (hyphophores). C. <i>V. vulgaris</i> , Brazil [22145]. D. <i>V. aff. vulgaris</i> , Brazil [23047]. E. <i>V. albopruinosus</i> , Ecuador. F. <i>V. vulgaris</i> , Brazil [23052].	134
Capítulo 3:	
Figure 1: The molecular reference tree (maximum likelihood tree) showing 36 genus-level lineages of Gomphillaceae and the relationships among genera. The molecular phylogenetic analysis presented and confirmed 13 new genera e four newly reinstated genera for the family. ...	144
Figure 2–5: Result of the method of morphology-based phylogenetic binning using taxa in the molecular reference and taxa based os their phenotype characters. The analysis include node identifications (ID) number and bootstrap support numbers after the query name from the RAxML analysis	145

Capítulo 4:

Figure 1. Habit of the new species (holotypes). A–D. *Gyalideopsis aptrootii*. A. Apothecia. B. Hyphophores. C. Margin of hyphophore showing partially translucent hyphal scales. D. Moniliform diahyphal bunches. E–F. *G. marcellii*. E. Hyphophores. F. Filiform diahyphae. Scale in A, B, E=1 mm; in C, D, F=20 μm235

LISTA DE TABELAS

Capítulo 1:

Table 1. GenBank accession numbers and voucher information (for newly generated sequences) for the taxa used in this analysis.65

Capítulo 3:

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. Node identifications (ID) are listed for each node and the final genus placement is indicated for each species. Genus placement is consistent for a taxon and therefore might not be the same as Node ID in alternative node placements with low support. In cases where the placement was not resolved or some conflict was detected, we adopted a conservative genus placement which is indicated in brackets.144

Capítulo 4:

Table 1. List of species of *Gyalideopsis* known from Brazil, with reporting sources indicated in parentheses and distribution in Brazilian states given. AP=Amapá, BA=Bahia, CE=Ceará, DF=Distrito Federal, ES=Espírito Santo, GO=Goiás, MG=Minas Gerais, MS=Mato Grosso do Sul, MT=Mato Grosso, PB=Paraíba, PE=Pernambuco, PR=Paraná, RJ=Rio de Janeiro, RO=Rondônia, RS=Rio Grande do Sul, SC=Santa Catarina, SE=Sergipe, SP=São Paulo. Asterisks indicate species originally described from Brazil, with two asterisks indicating species not yet known from outside the country.232

Sumário

1. INTRODUÇÃO GERAL	19
1.1 Líquens	19
1.2 Aspectos gerais sobre líquens foliícolas	20
1.3 Estudo de líquens foliícolas neotropicais	21
1.4 Estudo de líquens foliícolas no Brasil	23
1.5 Família Gomphillaceae	26
1.4 Justificativa	29
2. OBJETIVOS	30
2.1 Objetivo Geral	30
2.2 Objetivos Específicos	30
3. METODOLOGIA	34
3.1 Áreas de estudo	34
3.2 Coleta de dados	44
3.3 Processamento e identificação das amostras líquênicas	44
3.4 Extração, Purificação e Sequenciamento das amostras	45
3.5 Alinhamento das sequências e análises filogenéticas	47
4. RESULTADOS	47
5. CONCLUSÕES GERAIS	48
5. REFERENCES	48
Capítulo 1	59
1. INTRODUCTION	61
2. MATERIALS AND METHODS	64
2.1 Taxon sampling	64
2.2 Molecular methods	64
2.3 Sequence alignment	64
2.4 Phylogenetic analysis	65
3. RESULTS	65
4. DISCUSSION	81
5. REFERENCES	86
Capítulo 2	90
1. INTRODUCTION	93
2. MATERIALS AND METHODS	96
3. RESULTS AND DISCUSSION	96
4. REFERENCES	135
Capítulo 3	137
1. INTRODUCTION	139
2. MATERIALS AND METHODS	141
2.1 Phenotype data	141
2.2 Molecular reference tree	142

2.3 Phylogenetic binning	142
3. RESULTS.....	142
4. DISCUSSION.....	149
5. REFERENCES	151
Capítulo 4.....	227
1. INTRODUCTION	229
2. MATERIAL AND METHODS	231
3. RESULTS AND DISCUSSION.....	231
4. LITERATURE CITED	247

1. INTRODUÇÃO GERAL

1.1 Líquens

Representantes do filo Ascomycota são encontrados em todos os ecossistemas terrestres e algumas linhagens são aquáticas em ambientes de água doce e marinhos (Jaklitsch *et al.* 2016). Dentre os representantes do filo, os líquens foliícolas, comparados com outros organismos, têm várias vantagens para serem estudados, incluindo a alta susceptibilidade ante fatores microclimáticos, o crescimento bidimensional, o bom conhecimento taxonômico, a fácil coleta, documentação e rápido desenvolvimento das comunidades, além da sua grande diversidade, particularmente nas florestas de planícies, onde outras epífitas são geralmente escassas (Lücking 1997a).

Além disso, os Ascomycota representam o maior filo dentro do reino Fungi, com aproximadamente 65.000 espécies conhecidas, e as associações liquenizadas com algas e/ou cianobactérias representam um dos principais e bem-sucedidos estilos de vida com mais de 19.000 espécies e quase 1.000 gêneros (Feuerer & Hawksworth 2007; Kirk *et al.* 2008; Jaklitsch *et al.* 2016; Lücking *et al.* 2017). O aumento na descrição de espécies novas dentro do reino Fungi, principalmente a partir de 2010 com 1.800 espécies por ano, é largamente atribuído ao uso crescente de técnicas moleculares (Hawksworth & Lücking 2017).

Aproximadamente 20% das espécies de fungos conhecidas são encontradas na natureza associadas simbioticamente a algas ou cianobactérias (Nash 2008; Kirk *et al.* 2008). Devido à associação resultante, os líquens formam uma entidade morfológica com propriedades químicas e fisiológicas próprias, que é o talo liquênico (Ahmadjian 1965). Essa estrutura microbiana colaborativa é adaptada para exibir efetivamente simbioses fotossintéticas para captura de luz, protegendo-os e permitindo períodos suficientes de hidratação e troca gasosa (Sanders & De Los Ríos 2016).

Os líquens distinguem-se de outras simbioses fungo-planta por apresentar um fotobionte com plano corporal de microalgas principalmente indiferenciadas, unicelulares a multicelulares, diferentemente do encontrado em macroalgas, briófitas e plantas vasculares envolvidas em associações fúngicas (Lücking *et al.* 2017). Os líquens podem ser organizados quanto ao seu substrato, incluindo o córtex de vegetais superiores (corticícolas), rocha (saxícolas), terra (terrícolas), madeira (lignícolas) e folhas (foliícolas). Os líquens foliícolas são geralmente crostosos e parcialmente ligados ao substrato (Carlile *et al.* 2001; Deacon

2006; Nash 2008). Crescem sobre as superfícies das folhas de plantas vasculares (arbustos, árvores e epífitas), completando seu ciclo de vida rapidamente devido a sua natureza efêmera (Lücking 2001, 2008a, Lücking *et al.* 2009).

1.2 Aspectos gerais sobre líquens foliícolas

Os líquens foliícolas são fungos liquenizados que habitam folhas de plantas vasculares em florestas tropicais. Em relação a sua distribuição, são essencialmente limitados às florestas tropicais, com poucas espécies ocorrendo em habitats muito úmidos de regiões subtropicais e temperadas (Lücking 1999a, 2001, 2008).

Remanescentes de Mata Atlântica conservam uma parte importante de toda diversidade desse grupo, mostrado por Cáceres *et al.* (2000). Neste tipo de vegetação, as folhas são de vida curta e proporcionam um ambiente efêmero não excedendo 24-36 meses de vida, mesmo em florestas tropicais, porém são perenes (Lücking *et al.* 2009). As comunidades de líquens foliícolas não se desenvolvem em plantas que perdem suas folhas anualmente, como as árvores que dominam as florestas temperadas e florestas estacionais decíduais tropicais secas, já que necessitam de uma camada polissacarídica (mucilagem) para aderir à superfície da folha, e elevado nível de umidade imprescindível ao seu desenvolvimento (Lücking *et al.* 2009). Os líquens foliícolas crescem na superfície superior da folha (epífilos), e raramente são hipófilos, crescendo na superfície inferior (Lücking 2001).

A maioria dos gêneros de líquens foliícolas é encontrada em outros substratos (Farkas & Sipman 1993). Mesmo diante disso, os líquens foliícolas não apresentam rizinas ou outros apressórios típicos dos líquens não foliícolas, proporcionando uma penetração na superfície da folha sem causar prejuízos, principalmente quanto ao desempenho fotosintético (Lücking 2001). Porém, em pelo menos alguns casos, o crescimento de representantes foliícolas do gênero *Strigula* parece causar danos ao tecido foliar, devido ao fotobionte *Cephaleuros* (Trentepohliaceae) ser considerado um semiparasita em tecidos foliares no estágio não-liquenizado (Lücking 2001, 2008).

A reprodução sexuada dos líquens foliícolas é principalmente por via ascomata e ascósporos. Com base na sua morfologia funcional, os ascomas podem ser divididos em dois tipos básicos: apotécios com um himênio exposto e peritécios com um himênio fechado. A reprodução assexuada é por via de conidiomas que formam conídios, sendo encontrada em muitos líquens foliícolas como estratégia de dispersão através dos picnídios, campilídios ou hifóforos. Os hifóforos são considerados órgãos especializados de reprodução assexuada restritos à família Gomphillaceae, produzindo hifas que servem como conídios e foram

inicialmente descritos por Batista e seus colaboradores como partes dos líquens foliícolas (Santesson 1952; Sérusiaux 1986; Sérusiaux & De Sloover 1986; Lücking 1997a; Ferraro 2004; Lücking 2008b).

Em relação à distribuição, poucos líquens foliícolas ocorrem a altas altitudes, mesmo sabendo que estes contribuem significativamente para diversidade total. As vegetações subtropicais e temperadas também não promovem um habitat ideal para líquens foliícolas, como apresentado no trabalho de Herrera-Campos *et al.* (2004) no qual locais montanhosos usualmente têm pouca abundância de líquens foliícolas.

Até 2008, a riqueza mundial dos líquens de hábito foliícola era mais de 800 espécies (Lücking & Cáceres 2006; Lücking 2008b), sendo 616 espécies e 15 táxons subespecíficos ocorrendo nos Neotrópicos, do sul dos Estados Unidos e México ao norte do Chile e Argentina, como também os bosques pluviosos temperados da região da Valdivia no sul do Chile e Argentina, os quais são regiões que representam a monografia de Lücking (2008b). Nesse contexto, é provável que muitas espécies permaneçam não descritas, tendo em vista que áreas recém exploradas sempre apresentam novas taxa para a ciência (Farkas & Sipman 1993). Mesmo com inúmeras espécies não descritas, alguns trabalhos vêm desenvolvendo pesquisas de descrição de espécies foliícolas para o mundo (Aptroot & Cáceres 2013; Van DenBroeck *et al.* 2014; Seavey & Seavey 2014), o que pode resultar num aumento significativo no número de espécies, como determinado por Lücking (2008b).

Porém, sabendo que os líquens foliícolas ocorrem muitas vezes em abundância em um determinado local, podendo estarem ausentes em outro com condições ambientais aparentemente similares, um fenômeno que pode ser devido aos modos de dispersão dos líquens ou aspectos históricos da localidade (Lücking 1999a).

Dessa forma, espera-se uma riqueza significativa para o Brasil, tendo em vista que outros fatores estão relacionados à diversidade de espécies para uma determinada área, tais como altitude, grau de sazonalidade e respostas as condições climáticas (Lücking 1999a; Lücking 2001).

Além disso existe a dificuldade taxonômica, em que inventários completos de epífitos tropicais não-vasculares, particularmente líquens, ainda não foram realizados (Lücking & Matzer 2001).

1.3 Estudo de líquens foliícolas neotropicais

Para Cáceres & Lücking (2006), a história dos estudos dos líquens foliícolas nos neotrópicos, que inclui o Brasil, pode ser dividida em quatro fases: o período inicial,

dominado pelos inúmeros trabalhos de Müller Argoviensis; a monografia de Santesson (1952); a fase brasileira, entre 1960 e 1975, representada pelo micologista A. C. Batista e colaboradores; e por fim, a fase moderna, com início da década dos anos 70.

Baseado na história dos líquens foliícolas, uma importante descrição cronológica desse grupo foi feita por Farkas & Sipman (1993), na qual destaca os principais liquenólogos e suas principais descobertas desde 1823, quando o primeiro líquen foliícola, gênero *Strigula* Fr., foi descrito por Elias Fries (Papong *et al.* 2007), até a década de 90.

No ano seguinte à descrição do primeiro líquen foliícola, Feé (1824), foi o primeiro a tratar os grupos de líquens foliícolas em detalhe, descrevendo e ilustrando 13 espécies em nove gêneros (Farkas & Sipman 1993). Décadas seguintes, mais precisamente entre os anos de 1890 e 1926, Vainio descreveu outras 40 espécies, sendo reconhecido como o autor mais importante antes da monografia de Santesson em relação aos líquens foliícolas em geral, tendo, em seguida, seu trabalho prosseguido por Zahlbruckner, Malme e Schilling (Vainio 1890; Vainio 1896; Lücking 1997; Farkas & Sipman 1993).

Outros grandes pesquisadores que descreveram parte dos líquens foliícolas no século passado foram Montagne, Nylander, Babington, Leighton, Müller Argoviensis, Krempelhuber e Stirton (Farkas & Sipman 1993).

Para Papong *et al.* (2007), Elias Fries pode ter sido o primeiro a mencionar os líquens foliícolas, mas foi Santesson (1952) quem descreveu o primeiro líquen através da monografia desse grupo, sendo até hoje utilizado como um guia útil para a taxonomia de líquens foliícolas. Além disso, Santesson (1952) centralizou os estudos nos líquens obrigatoriamente foliícolas já que, através de sua revisão taxonômica, 236 espécies foram reconhecidas em 38 gêneros, pertencentes a 10 famílias. Adicionalmente, seu trabalho realizou consideráveis reorganizações, sendo 67 novas combinações, 747 novos sinônimos e descreveu 44 novas espécies e dois novos gêneros (*Lasioloma* e *Phyllophiale*) (Farkas & Sipman 1993).

Ao longo dos anos muitos trabalhos vêm apresentando descrições de novas espécies de líquens foliícolas em todo o mundo. Lücking (1991, 1992) descreveu 15 novas espécies para a Costa Rica. No ano de 1999a, Lücking descreveu sete novas espécies e uma nova variedade em uma revisão taxonômica de espécies de líquens foliícolas das famílias Asterothyriaceae e Thelotremaaceae na Costa Rica e uma variedade. Outro trabalho desenvolvido por Lücking (1999b), foi uma revisão taxonômica da família Gyalectaceae na Costa Rica com três novas espécies descritas. Em Etayo & Lücking (1999), uma nova espécie de líquen foliícola foi descrita para Guiana.

Para o México, Herrera-Campos & Lücking (2003) descreveram cinco novas espécies de líquens foliícolas, pertencentes à família Gomphillaceae. No ano seguinte, estes autores revelaram um total de 288 taxa de líquens foliícolas, que, somado a outros trabalhos para a área, totalizou 293 (Herrera-Campos *et al.* 2004). Desses, 29 foram novas espécies para ciência e pertencem aos gêneros *Arthonia* Ach., *Byssoloma* Trevis., *Enterographa* Fée, *Gyalectidium* Müll. Arg., *Gyalideopsis* Vezda, *Malmidea* Kalb, Rivas Plata & Lumbsch, *Opegrapha* Ach., *Phylloblastia* Vain., *Porina* Ach., *Psoroglaena* Müll.Arg., *Pyrenothrix* Riddle e *Tricharia* Fée.

Para Cáceres & Lücking (2006), e levando em consideração o ano do trabalho, como países México, Costa Rica, Equador, as Guianas, Brasil e Argentina distinguem-se entre os melhor estudados. Por outro lado, Guatemala, El Salvador, Nicarágua, Panamá, Colômbia, Venezuela, Peru, Guiana Francesa e Suriname possuem coleções mais escassas. Para a América tropical, muitas espécies de líquens foliícolas são amplamente distribuídas a partir do sul dos Estados Unidos até o norte do Chile e Argentina (Lücking 2001).

De acordo com Lücking (2008b), a biota neotropical de líquens foliícolas compreende 74 gêneros em 23 famílias e oito ordens. O maior número tem sido registrado para Costa Rica com aproximadamente 400 espécies, o que seria esperado já que se estima que a diversidade de líquens para o país seja de 4.000 taxa, seguida pelo Brasil e Equador com 336 e 275 espécies, respectivamente (Herrera-Campos *et al.* 2004). Em termos de quantidade de espécies de líquens foliícolas, Herrera-Campos *et al.* (2004) mostraram que o México é o terceiro maior para os Neotrópicos. Para o Equador, atualmente, Etayo (2017) descreveu um novo gênero liquenícola *Paragyalideopsis*, com quatro espécies incluídas, pertencente à família Gomphillaceae

Mesmo diante desses resultados, é esperado que o Brasil apresente um número tão significativo da riqueza liquênica quanto a Costa Rica, não apenas por seu tamanho territorial, mas por apresentar Florestas tropicais que são famosas por sua alta biodiversidade, o que deve incluir os líquens foliícolas (Lücking 2001).

1.4 Estudo de líquens foliícolas no Brasil

A história dos líquens foliícolas para o Brasil iniciou-se com Müller Argoviensis, entre 1882 a 1892, como mostram Farkas & Sipman (1993) através de um gráfico com os principais picos anuais de novas espécies de líquens foliícolas descritas até aquele momento. Porém, os estudos de Müller Argoviensis com os foliícolas iniciaram antes, tendo em vista que o gênero

Gyalectidium, parte da família Gomphillaceae, foi estabelecido por este autor em 1881, para um grupo de três espécies novas: *G. dispersum* Müll. Arg., *G. filicinum* Müll. Arg. e *G. xantholeucum* Müll. Arg. (Ferraro *et al.* 2001). O conhecimento dos líquens foliícolas até a metade do século 20 foi resumido por Santesson (1952), citando numerosas espécies para o Brasil.

O micologista Augusto Chaves Batista, fundador do Instituto de Micologia da Universidade de Recife, destacou-se no final dos anos 50, na chamada fase brasileira (Cáceres & Lücking 2006). Nesse tempo, poucas pessoas tinham consciência que o grupo de Batista tinha iniciado um estudo de líquens foliícolas não-liquenizados e liquenizados na região Amazônica (Estados de Roraima, Amazonas, Rondônia, Amapá, Pará e Maranhão) e do Estado de Pernambuco, na Região Nordeste (Lücking *et al.* 1998, 1999). Entre 1960 a 1975, Batista e co-autores descreveram taxa novos para o Brasil, publicando em torno de 250 nomes de líquens foliícolas, dentre eles 38 gêneros e 69 espécies novas (Lücking *et al.* 1999; Farkas & Sipman 1993; Cáceres & Lücking 2006). As coleções de Batista, de acordo com os arquivos do URM, compreenderam um total de 107 gêneros e 357 espécies de líquens foliícolas (incluindo nomes não publicados), sendo confirmados em 47 gêneros e 143 espécies (Lücking *et al.* 1998). Batista e seu grupo acumularam cerca de 43.000 coleções de fungos não liquenizados e liquenizados, com um total de mais de 80.000 espécimes, no qual, aproximadamente, 18.000 referem-se a líquens foliícolas (Lücking *et al.* 1998).

Nos anos 60, o liquenólogo A. Vězda começou a estudar em detalhe os líquens foliícolas. Em 1966, descreveu o gênero *Gyalidea* Lettau ex Vězda. Em Vězda & Poelt (1987), nove gêneros foram inseridos na família Gomphillaceae, antes pertencendo a Asterothyriaceae (*Aulaxina* Fée, *Calenia* Müll. Arg., *Echinoplaca* Fée, *Gyalectidium* Müll. Arg., *Gyalideopsis* Vězda, *Tricharia* Fée e *Actinoplaca* Müll. Arg.), e dois gêneros descritos: *Bullatina* Vězda & Poelt e *Caleniopsis* Vězda & Poelt. Além desses trabalhos, Vězda tem papel importante no desenvolvimento de pesquisas para a família Gomphillaceae, com descrição de gêneros e espécies, além de trabalhos relacionados aos hifóforos, característica única da família (Vězda 1972; Vězda 1979; Kalb & Vězda 1988; Thor & Vězda 1984; Vězda 2003; Lücking *et al.* 2005). Entre 1976 e 1992, E. Sérusiaux descreveu 21 espécies de diferentes áreas geográficas, como também apresentou sínteses dos novos resultados mais importantes para pesquisa ecológica em líquens foliícolas (Farkas & Sipman 1993, Lücking & Cáceres 2006).

Desde a revisão do material brasileiro publicado por Batista e colaboradores, em particular W. de A. Cavalcante, L. Xavier Filho, J. L. Bezerra, D. J. M. Poroca, Lücking *et al.*

(1998) descreveram duas espécies novas, *Bapalmuia verrucosa* Sérus. & Lücking e *Enterographa batistae* Lücking & Sérus, e apresentaram 39 gêneros novos determinados por Batista e seus colaboradores. Além disso, reportaram novos registros de líquens foliícolas para o Brasil, tais como *Badimia galbinea* (Krempelh.) Vězda, *Calopadia subcoerulescens* (Zahlbr.) Vězda, *Echinoplaca marginata* Lücking, *Echinoplaca verrucifera* Lücking, *Fellhanera verrucifera* Lücking, *Mazosia bambusae* (Vain.) R. Sant., *Porina rubrosphaera* R. Sant.; *Trichothelium argenteum* Lücking & Ferraro e *Trichothelium sipmanii* Lücking.

No ano seguinte, Lücking *et al.* (1999) realizaram outra revisão nomenclatural e taxonômica dos nomes determinados por Batista *et al.*, e identificação dos espécimes não registrados de líquens foliícolas, relacionado as coleções para o estado de Pernambuco no herbário URM. Nessa revisão, os autores constataram três gêneros considerados “nomes duvidosos” *Aciesia* Bat., *Asbolisiomyces* Bat. & H. Maia e *Didymopycnomyces* Cavalc. & A. A. Silva; e 16 novas combinações: *Acleistomyces* Bat. = *Sporopodium* Mont., *Actinoteichus* Cavalc. & Poroca = *Asterothyrium* Müll. Arg., *Byrsomyces* Cavalc., *Chaetomonodorus* Bat. & H. Maia e *Scutomyces* J. L. Bezerra & Cavalc. = *Microtheliopsis* Müll. Arg., *Cyrta* Bat. & H. Maia = *Calopadia* Vězda, *Microxyphiomyces* Bat., Valle & Peres e *Psathyromyces* Bat. & Peres = *Tricaria* Fée; *Pycnociliospora* Bat. e *Raciborskiella parva* L. Xavier = *Strigula* Fr.; *Pyriomyces* Bat. & H. Maia = *Byssoloma* Trevis., *Septoriomyces* Cavalc. & A. A. Silva = *Phyllobathelium* Müll. Arg., *Sporocybomyces* H. Maia = *Echinoplaca* Fée, *Stephosia* Bat. & H. Maia = *Phyllophiale* R. Sant., e *Tauromyces* Cavalc. & A. A. Silva = *Gyalectidium* Müll. Arg. A distribuição geográfica desses novos gêneros descritos está em sua maioria para o estado do Amazonas, seguido de Rondônia, Pernambuco, Amapá e Maranhão.

Ainda em Pernambuco, e no mesmo ano, Cáceres (1999) desenvolveu um estudo voltado para diversidade, ecogeografia e conservação de líquens foliícolas na Mata Atlântica do estado, fornecendo dados ecológicos e listas de nomes de espécies identificadas durante a pesquisa. Além das 134 espécies presentes nas exsicatas do herbário URM, Cáceres (1999) revelou a existência de 75 espécies adicionais, resultando assim em mais de 200 táxons presentes nos remanescentes da Mata Atlântica de Pernambuco, Brasil. Esta foi a primeira pesquisa com novas coletas de líquens foliícolas no Nordeste brasileiro depois da era de Batista, que também incluiu o descobrimento de espécies novas para a ciência (Cáceres 1999b, Cáceres & Lücking 2000, Lücking & Cáceres 1999).

Alguns *checklists* também incluem referências para o Brasil, como os disponibilizados online por Lücking *et al.* 2000a; b, Lücking & Kalb (2000) e Farkas & Sipman (1993) com

uma lista de espécies foliícolas a partir de registros bibliográficos de 324 artigos científicos publicados posteriormente à pesquisa de Santesson (1952).

Trabalhos de descrição de espécies para o Brasil foram apresentados por Ferraro & Lücking (2003) para o estado do Mato Grosso, com o líquen *Gyalectidium aurelii* L.I Ferraro & Lücking, pertencente a Gomphillaceae. Lücking & Cáceres (2002) desenvolveram um trabalho de líquens foliícolas na Estação Científica Ferreira Penna, em Caxiuanã, Pará e, posteriormente, Aptroot & Cáceres (2013) registraram líquens foliícolas para o estado de Rondônia, no Parque Natural Municipal de Porto Velho, Sítio de Buriti, Estação Ecológica de Cuniã, Fazenda São Francisco.

Lücking (2008b), com o trabalho de líquens foliícolas para a Flora Neotrópica, incluiu 375 espécies e 184 tipos para o Brasil, além de chaves de identificação a nível de família e gênero. Uma das últimas espécies foliícolas descritas foi *Calopadia erythrocephala* (Farkas & Flakus 2012).

Desde então, diversas pesquisas continuam a ser desenvolvidas e publicadas sobre a taxonomia e florística dos líquens foliícolas, assim como sua ecologia e uso como bioindicadores (Cáceres & Lücking 2006), tendo em vista que o uso dos líquens foliícolas como bioindicadores está relacionado com suas preferências específicas por certas condições ambientais e sua elevada diversidade em pequena escala (Cáceres 1999).

1.5 Família Gomphillaceae

A enorme diversidade morfológica da família Gomphillaceae Walt. Watson (Watson 1929) é refletida na vasta amplitude ecológica. Os líquens desta família são encontrados em todos os tipos de substratos, desde as superfícies rochosas e do solo até as briófitas, casca e folhas (Lücking 2008b). Porém, a maioria das espécies descritas até agora é foliícola, mas isso talvez se deva ao fato de que os membros das Gomphillaceae são mais facilmente coletados nas folhas vivas e são componentes importantes de comunidades de líquens tropicais (Lücking *et al.* 2005; Lücking 2008b).

As espécies de líquens foliícolas possuem certas características morfológicas em comum devido às suas preferências ecológicas, como o talo crostoso que está estreitamente ligado ao substrato, fazendo-se necessário o conhecimento da sua morfologia e anatomia para identificação e para compreender as relações evolutivas e biológicas do grupo (Lücking 2008). No caso da família Gomphillaceae, as principais características dos grupos são as estruturas especiais presentes no talo como setas (**Fig. 01**) e pelos, sendo que a maioria das espécies produz conidiomas muito particulares chamados hifóforos. Estes, únicos da família

Gomphillaceae e não ocorrem em nenhum outro grupo de fungos, consistem de pedúnculo e ápice que produz conídios filiformes ou moniliformes (**Figs. 2A–C**). Outro tipo de conidioma presente em Gomphillaceae são os campilídios, caracterizados por possuir uma camada conidiógena e é parcialmente exposta e parcialmente coberta por um lóbulo de simetria bilateral (Cáceres 1999; Lücking *et al.* 2005; Lücking 2008).

Quanto à estrutura do talo, um estudo desenvolvido por Sanders & De Los Ríos (2016) mostrou que todas as espécies examinadas na pesquisa, e pertencentes a família Gomphillaceae, formavam talos crostosos muito finos e posicionados inteiramente acima da cutícula da folha, sem componentes vistos penetrando dentro ou abaixo desta camada. A construção do talo era simples e as mesmas características anatômicas básicas eram compartilhadas entre os diferentes espécimes estudados. Somado a isso, o talo em Gomphillaceae apresenta quatro principais características: incrustação com cristais de oxalato de cálcio, bem como a formação de setas, protalos e um córtex celular (Lücking *et al.* 2005). Esses talos são encontrados em vários substratos, mas, na maioria das vezes, são foliícolas e crostosos (Lücking 2008).

Em relação aos seus ascomas (**Fig. 3**), a família Gomphillaceae é caracterizada por sua anatomia apotecial, com paráfises finas, ricamente ramificadas e anastomasadas e ascósporos transversalmente septados a frequentemente muriformes e hialinos (**Figs. 2D–F**) Esse tipo de esporos é uma característica que ocorre em basicamente todos os gêneros, sendo considerada de longe a mais homoplástica de todas as características do grupo, o qual também apresenta um dos maiores graus de variação na morfologia apotecial (Lücking *et al.* 2005, 2007; Lücking 2008).

Quanto à ecologia, Gomphillaceae é bastante variável quanto à sua natureza biológica e preferências de substrato (Lücking *et al.* 2005), porém a enorme radiação dentro da família está claramente relacionada à evolução do hábito de crescimento foliícola (Lücking *et al.* 2005). Algumas espécies são consideradas liquenícolas, que crescem sobre outros líquens, e produzem apotécios e hifóforos tipicamente encontrados nos gêneros que os pertencem (Lücking 1997a; Lücking & Sérusiaux 1998; Lücking & Kalb 2002; Lücking *et al.* 2005).

A ordem Ostropales corresponde a quase 30% da diversidade global de líquens foliícolas e, por outro lado, são poucas as espécies foliícolas pertencentes a esse grupo, o que se deve ao fato de que muitas famílias desta ordem serem principalmente extratropicais e contem macrolíquens foliosos e fruticosos que não permitem o hábito foliícola (Lücking & Cáceres 2006). Em relação às famílias de líquens foliícolas, as mais representativas são Pilocarpaceae (ordem Lecanorales) e Gomphillaceae (ordem Ostropales) com 29 e 24

gêneros, respectivamente (Lücking 2008; Lücking *et al.* 2017). Os gêneros, *Porina* (Porinaceae), *Felhanera* (Pilocarpaceae) e *Byssoloma* (Pilocarpaceae) são os primeiros, segundo e o terceiro maiores gêneros entre os líquens foliícolas, respectivamente (Lücking & Cáceres 2006). Outro gênero representativo é o *Gyalideopsis*, que a partir das chaves de identificação para o mundo, atualmente se conhecem 94 táxons e é considerado o um dos gêneros com maior número de espécies liquenizadas foliícolas (Lücking *et al.* 2006; Lücking *et al.* 2017).

Atualmente, a família Gomphillaceae compreende 418 espécies descritas e 24 gêneros, incluindo os gêneros *Gyalidea* e *Asterothyrium*, anteriormente incluídos na família Asterothyriaceae, que forma parte do complexo familiar que também inclui a família Graphidaceae (Baloch *et al.* 2010; Rivas Plata *et al.* 2012; Lücking *et al.* 2017). Desse total de gêneros atualmente reconhecidos, apenas 15 apresentam-se geneticamente sequenciados (Lücking *et al.* 2017).

Apesar de sua importância para a diversidade tropical liquênica, considerada uma das maiores famílias de líquens foliícolas por suas peculiaridades morfológicas, a filogenia e taxonomia de Gomphillaceae têm sofrido significativas mudanças que são, em grande parte, desconhecidas (Lücking *et al.* 2004; 2005; 2007). Os estudos referentes a Gomphillaceae ainda são escassos, não havendo conhecimento extenso sobre a estrutura e posição filogenética da família. Várias espécies novas foram descobertas nos últimos anos (Herrera-Campos & Lücking 2002, 2003; Lücking *et al.* 2000; Oliveira *et al.* 2002), porém estudos mais profundos e recentes foram realizados apenas nos gêneros *Gomphillus*, *Gyalectidium* e *Gyalideopsis* (Ferraro *et al.* 2001; Ferraro & Lücking 2005; Lücking & Sérusiaux 2005; Lücking *et al.* 2006; Menezes *et al.* 2013; Xavier-leite *et al.* 2018).

Lücking & Kalb (2002) apresentaram *Asterothyrium septemseptatum* subsp. *africanum* Lücking & Kalb e *Aulaxina aggregata* Lücking & Kalb como espécies novas para a ciência, bem como 74 espécies de líquens foliícolas para o Kênia. Para a Costa Rica, Lücking *et al.* (2006), apresentaram a primeira avaliação do gênero *Gyalideopsis* e descreveram cinco espécies novas: *G. altamirensis* Lücking & Umaña, *G. macarthurii* Lücking, Umaña & Aptroot, *G. pseudoactinoplaca* Lücking & Chaves, *G. wesselsii* Lücking, Sipman & Chaves, *G. sp.*, e uma para *Jamesiella chaverriae* Chaves, Umaña & Lücking, como também o registro de 29 novas taxa para a Costa Rica.

Para a América do Norte, e a partir de estudos da família Gomphillaceae, Lücking *et al.* (2007) apresentaram como novas espécies para a ciência *Arthotheliopsis floridensis* Lücking & W.R. Buck, *Echinoplaca areolata* Lücking & W.R. Buck, *Gyalectidium tuckerae*

Lücking & Lendemer, *G. viride* Lücking, W.R. Buck & Rivas Plata, *Gyalideopsis americana* Lücking & W.R. Buck, *G. ozarkensis* Lücking, W.R. Buck & R.C. Harris, *G. subaequatoriana* Lücking & W.R. Buck, *G. submonospora* Lücking & W.R. Buck, *Tricharia floridensis* Lücking & W.R. Buck, *T. subumbrosa* Lücking & W.R. Buck e *T. tuckerae* Lücking & W.R. Buck; além de variações e novos registros para o continente.

Para o Brasil, a família Gomphillaceae foi estudada por Augusto Chaves Batista e seu grupo que estabeleceram uma grande quantidade de táxons novos baseados em material do Nordeste e da Amazônia, inclusive vários novos gêneros de Gomphillaceae válidos até hoje, como *Aderkomyces* (Lücking *et al.* 1998; Lücking 2008b). Mais recentemente, Menezes *et al.* (2013) descreveram a espécie *G. ellipsoidea* para o estado do Ceará. Além de Santos *et al.* (2017), com novos registros para o Nordeste e Brasil e, para os estados de Santa Catarina e São Paulo. Outro trabalho considerado recente com descrições de espécies é o desenvolvido por Xavier-Leite *et al.* (2018) com duas espécies novas de Gomphillaceae, *Gyalideopsis aptrootii* e *G. marcelii*. Essas espécies, nesse caso, apresentaram hábito corticícola, mas, como explicado por Lücking *et al.* (2005), essa transição entre hábito de crescimento corticícola para um crescimento foliícola parece ter ocorrido dentro do gênero *Gyalideopsis*.

1.4 Justificativa

A família Gomphillaceae vem se destacando pela crescente descoberta de espécies e gêneros novos porém, sabe-se que ainda há muito o que desvendar no grupo. As pesquisas mais recentes para o grupo proporcionaram um aumento de 19 para 24 gêneros e atualizaram o número de espécies atualmente conhecidas para 418 (Lücking *et al.* 2005; Lücking *et al.* 2017). Algumas lacunas quanto à sistemática e filogenia do grupo precisam ser elucidadas, já que há ausência de evidências moleculares e poucos trabalhos filogenéticos desenvolvidos para a família Gomphillaceae, diferentemente de trabalhos de descrição de espécies e gêneros.

Outro fator importante é a contribuição de Gomphillaceae para a diversidade liquênica já que a diversidade da família no Brasil é muito alta e quase todos os gêneros e mais de 50% das espécies conhecidas mundialmente ocorrem nas áreas de estudo. Por apresentar uma ampla variedade em relação às suas estruturas reprodutivas, a família Gomphillaceae poderia ser um modelo para o estudo da evolução de ascomas e conidiomas dentro dos fungos, tornando o conhecimento da sua filogenia uma contribuição significativa em relação a isso (Lücking 1997a).

Considerados pontos importantes para o desenvolvimento deste trabalho, a grande quantidade de homoplasia e o baixo nível de correlação de características dos apotécios e

hifóforos reforçam a necessidade de uma abordagem molecular extensa que acabará por esclarecer a situação incerta da família (Lücking 2008).

Além da importância para a biodiversidade, os líquens desenvolvem importante papel na ecologia de florestas tropicais por se envolverem na ciclagem de nutrientes e retenção de água (Lücking 2001). Além do papel ecológico desenvolvido pelos líquens foliícolas, incluindo a família Gomphillaceae, que servem como bioindicadores de alterações ambientais e poluição atmosférica (Lücking 1997a, 2008a), especialmente nas áreas de Mata Atlântica, utilizando do conhecimento de sua filogenia na avaliação dos efeitos da fragmentação de áreas florestais.

Por fim, este trabalho vem expor a situação atual da sistemática e filogenia de líquens foliícolas representados pela família Gomphillaceae para o Brasil e Neotrópico, objetivando esclarecer as relações dentro grupo e estimular o desenvolvimento de outros estudos semelhantes. Inclusive, utilizando o método conhecido por “*binning phylogenetic*”, no qual espécies sem dados moleculares, apenas morfológicos, são analisados filogeneticamente com espécies sequenciadas a fim de tentar esclarecer a sistemática da grupo que, neste caso, será da família Gomphillaceae.

2. OBJETIVOS

2.1 Objetivo Geral

Revisar sistematicamente e filogeneticamente a família Gomphillaceae (*Ascomycota* liquenizados) usando caracteres morfológicos e moleculares, com enfoque nas linhagens foliícolas.

2.2 Objetivos Específicos

- ✦ Estabelecer uma filogenia da família Gomphillaceae usando os dois marcadores mtSSU e nuLSU;
- ✦ Comparar a filogenia molecular com um estudo prévio cladístico baseado no fenótipo e analisar quais clados concordam com os dois métodos e quais não;
- ✦ Descrever novas linhagens detectadas pela filogenia molecular formalmente como novos gêneros quando tem suporte e correlação com caracteres diagnósticos;
- ✦ Usar o método de '*binning*' filogenético para avaliar a posição de espécies não sequenciadas a nível global na nova classificação com os novos gêneros incluídos;
- ✦ Fazer um estudo de caso de uma revisão taxonômica para um gênero de Gomphillaceae no Brasil, usando o gênero *Gyalideopsis* como exemplo.

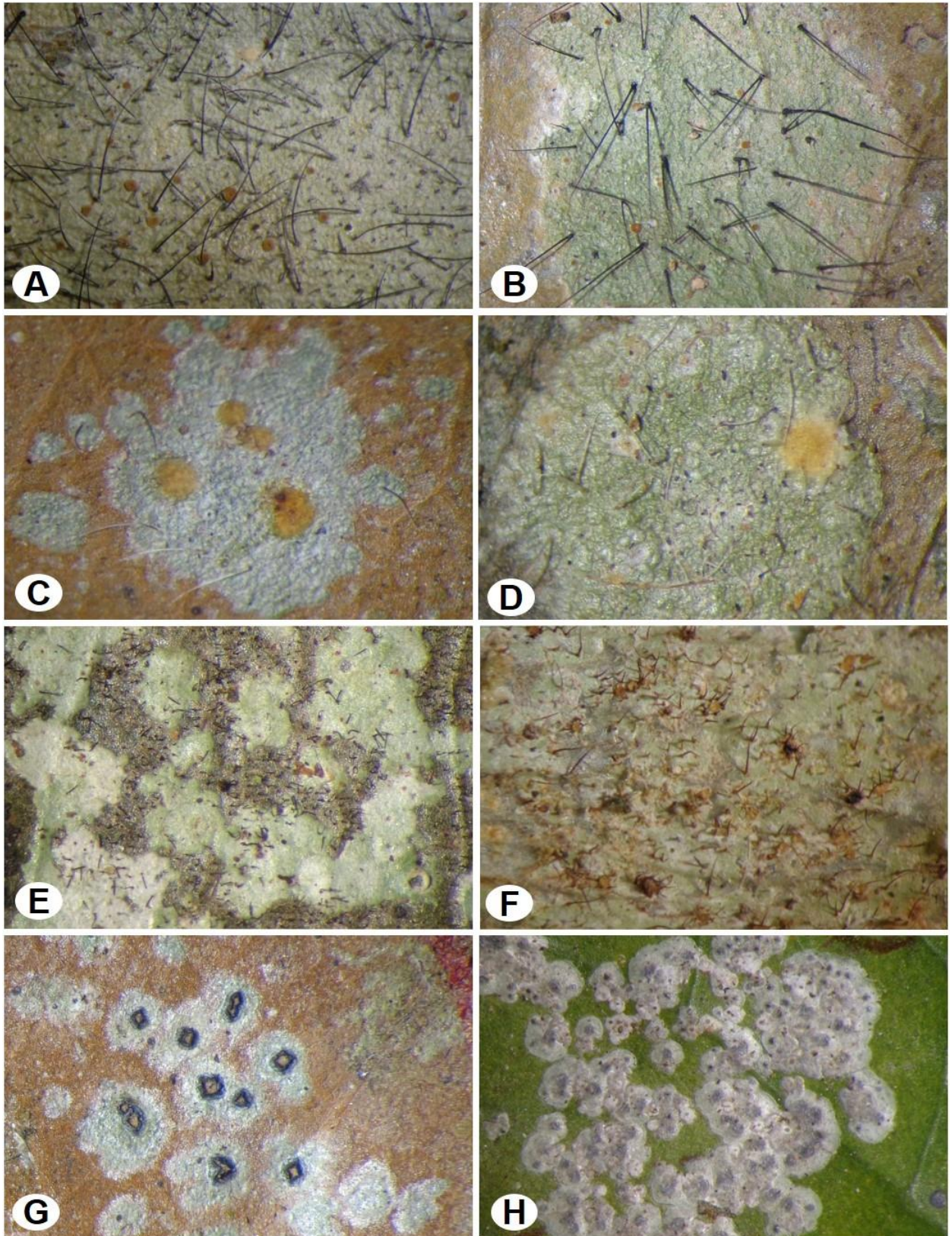


Figura 1: Diferentes cores de setas presentes nos talos da família Gomphillaceae. **A–B.** Setas pretas comumente encontradas em talos de *Tricharia*. **C–D.** Representantes do gênero *Echinoplaca* e a presença de setas brancas. **E–F.** Talos de *Caleniopsis* e *Rubrotricha*, respectivamente, com setas vermelhas. **G–H.** Exemplos de gêneros que não possuem setas, como *Aulaxina* e *Asterothyrium*, respectivamente.

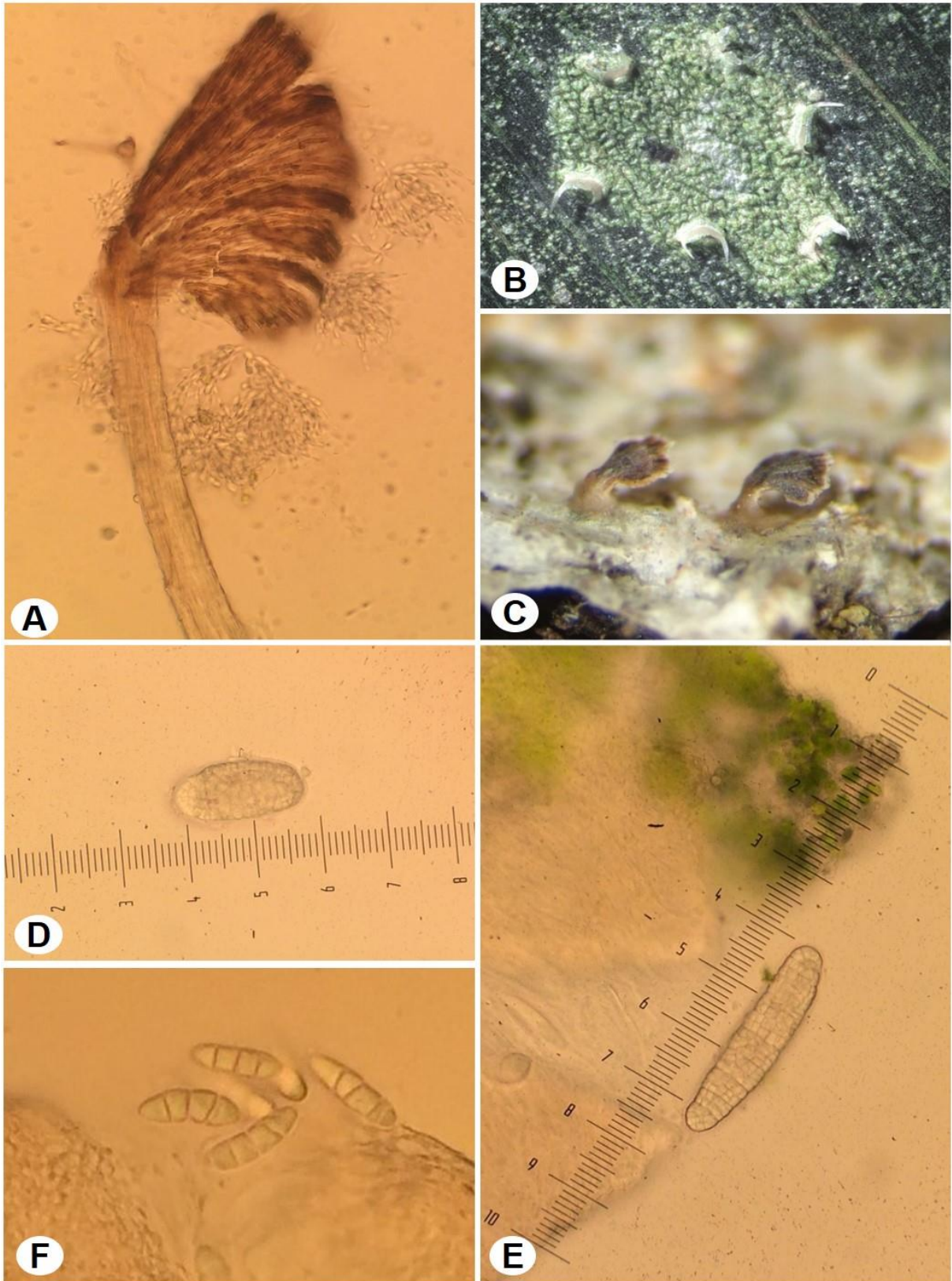


Figura 2: Hifóforos e esporos em espécies foliícolas da família Gomphillaceae. **A.** Estruturas microscópicas do hifóforo, pedúnculo e ápice, e as diahifas de *Psathyromyces* (nov. comb.). **B.** Hifóforos *squamiform* de *Gyalectidium filicinum*. **C–D.** Hifóforos *flabellate* e esporo muriforme hialino pertencentes ao gênero *Aderkomyces*. **E.** Esporo muriforme e hialino do gênero *Tricharia*. **F.** Esporo transversalmente septado e hialino do gênero *Aulaxina*.

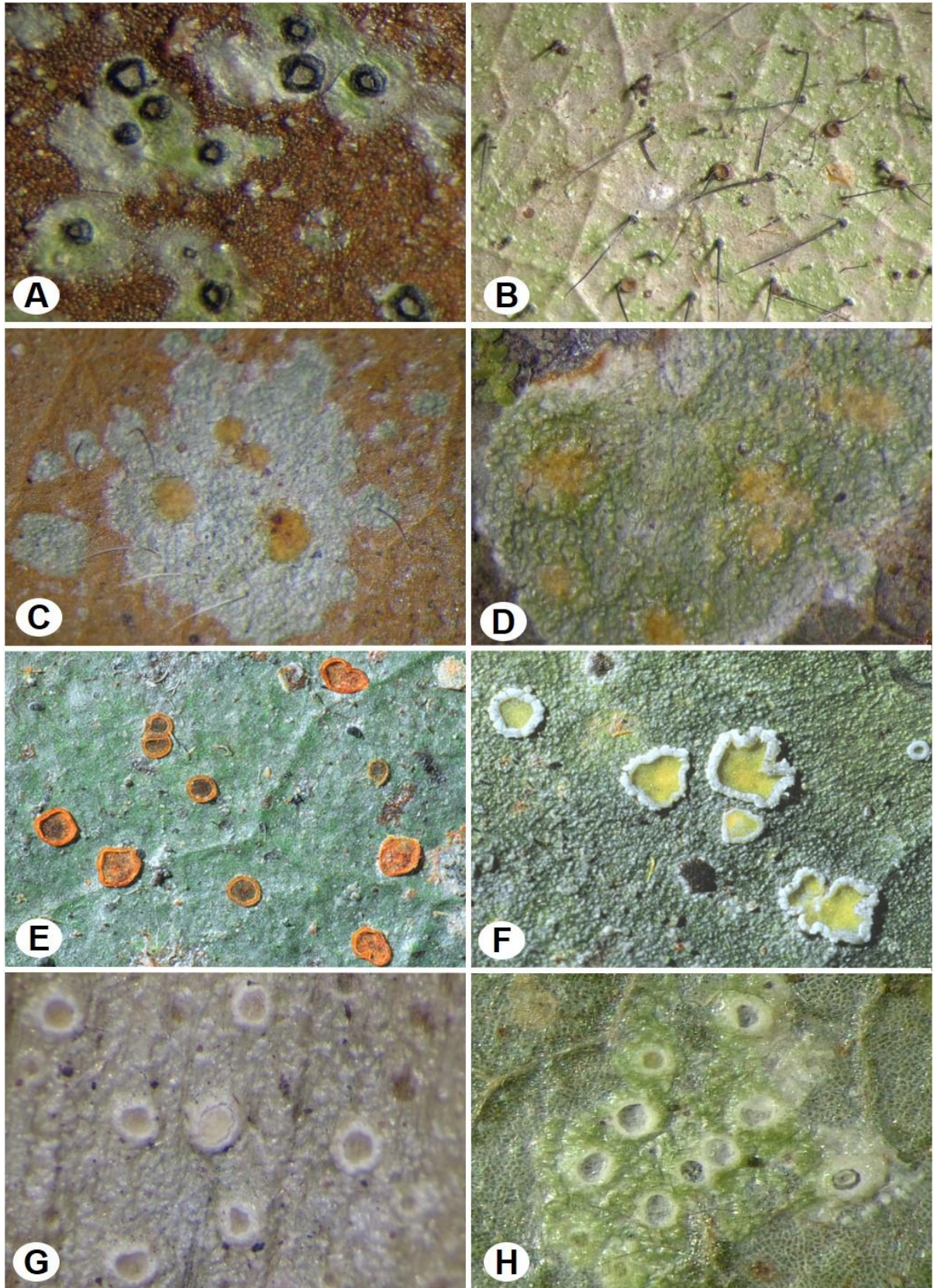


Figura 3: Diferentes tipos de apotécios encontrados na família Gomphillaceae. **A.** Apotécio erupente carbonizado de *Aulaxina*. **B.** Apotécio séssil de *Tricharia*. **C–D.** Apotécios *adnate* de *Echinoplaca*. **E–F.** Apotécios *appanate-sessile* pertencentes ao gênero *Gyalediopsis*. **G–H.** Apotécios *erupent-zeorine* do gênero *Gyalectidium*.

3. METODOLOGIA

3.1 Áreas de estudo

A coleta de líquens foliícolas foi realizada na região Nordeste, Sudeste e na Amazônia, mais precisamente nos seguintes estados: Amapá, Bahia, Paraíba, Pernambuco, Sergipe, Rio de Janeiro e Espírito Santo. Em cada estado foram escolhidas áreas equivalentes a Brejo de Altitude e Mata Atlântica, bem como uma área na Amazônia brasileira. Foram introduzidas nas análises amostras de líquens foliícolas coletadas na América Latina por Dr. Robert Lücking, provenientes da Guatemala, Costa Rica, Panamá, Cuba e Brasil. Adicionalmente, seqüências do GenBank oriundas do México, Suécia, Costa Rica, Nicarágua, Escócia e Brasil também foram utilizadas.

As coletas no Brasil em áreas de Brejo de Altitude foram realizadas no Parque Estadual Mata do Pau-Ferro (PB), Serra da Jibóia (BA), Brejo dos Cavalos (PE) e Serra da Guia (SE). Para a Mata Atlântica, foram visitadas a Reserva Biológica Guaribas (PB), Parque Nacional Serra de Itabaiana (SE), Parque Nacional do Itatiaia (PNI) (RJ), Reserva da Una (BA) e Estação Biológica Santa Lúcia (ES). Na Amazônia brasileira, as coletas foram realizadas na Floresta Nacional do Amapá e Reserva Extrativista do Maracá, ambas no estado do Amapá (**Fig. 4**). Segue abaixo uma breve descrição das áreas representadas pelas espécies utilizadas nas análises.

- **Brasil**

Parque Estadual Mata do Pau-Ferro, Paraíba

Unidade de Conservação (UC) de domínio estadual, também conhecida como Mata Pau-Ferro, está localizado na Microrregião do Brejo Paraibano ($6^{\circ} 58'S$ e $35^{\circ} 42'W$), com uma área de aproximadamente 600 ha, numa altitude variável entre 400 e 600 m (Barbosa *et al.* 2005; Andrade *et al.* 2006; Xavier-Leite *et al.* 2015) (**Figs. 5A–D**).

Serra da Jiboia, Bahia

A Serra da Jiboia localiza-se na latitude $12^{\circ}51'S$ e longitude $39^{\circ}28'W$, tem altitude compreendida entre 400-800 msnm, extensão de 6 km, e está inserida no município de Santa Terezinha, próximo ao limite do município Castro Alves, estado da Bahia, sendo circundada por uma área de caatinga e revestida na encosta por mata higrófila (Queiroz *et al.* 1996; Valente *et al.* 2009). No topo da serra, a altitude é de cerca de 750–800 msnm, apresentando

um afloramento gnáissico-granítico, sobre o qual se desenvolve uma vegetação de campo rupestre (Queiroz *et al.* 1996) (**Figs. 5E–H**).

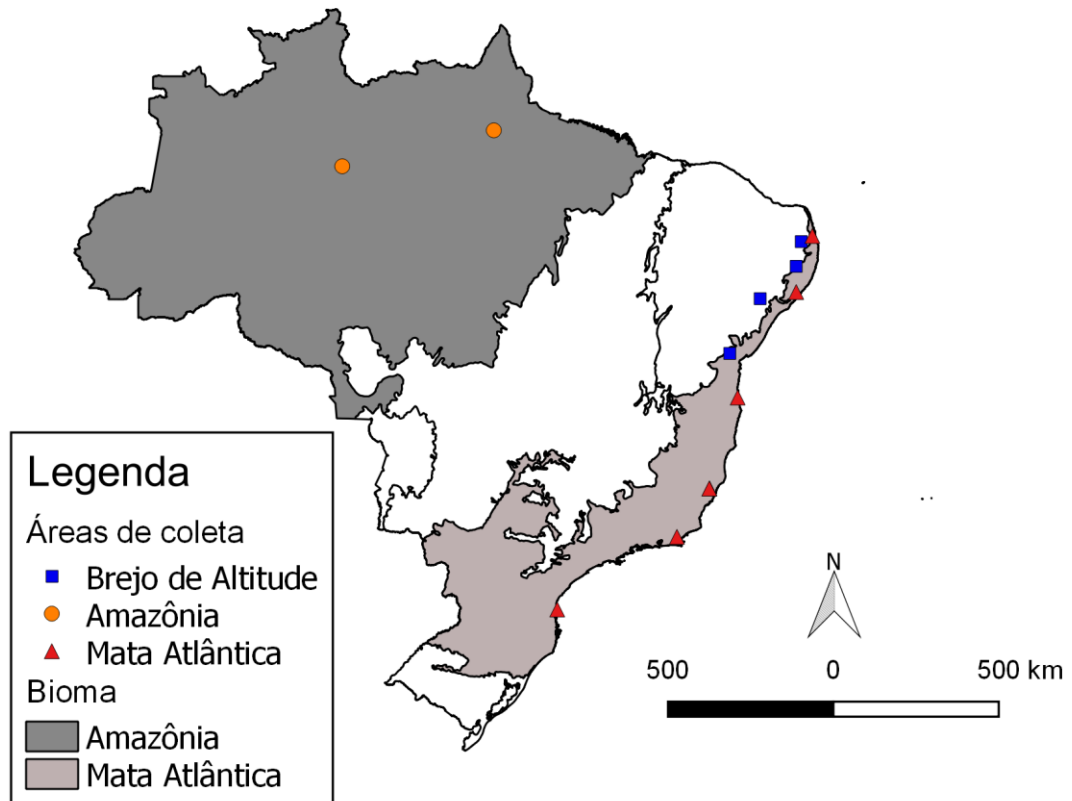


Figura 4: Mapa do Brasil com pontos de coletas de líquens foliícolas realizadas nas áreas de Mata Atlântica, Brejo de Altitude e Amazônia (Fonte: Paulo Fernandes).

Parque Ecológico Municipal João Vasconcelos Sobrinho, Pernambuco

Constitui um dos mais significativos remanescentes de Mata Atlântica, situando-se no município de Caruaru, PE (Braga *et al.* 2002), onde localiza-se o Parque Ecológico Municipal João Vasconcelos Sobrinho (8° 16' S, 35° 58' W) (Tabarelli & Santos 2004), também conhecido por Brejo dos Cavalos (**Figs. 6A–D**).

Serra da Guia, Sergipe

O ponto (09°58' S, 37°52' W) mais alto do estado de Sergipe, faz parte do Complexo Serra Negra e está localizado na fronteira das cidades de Poço Redondo (Sergipe) e Pedro

Alexandre (BA) (Machado *et al.* 2012). Esta é a parte mais alta de Sergipe, com altitudes de até 750 m de altitude e inclui a fonte do Rio Sergipe. O clima é semi-árido, com média precipitação anual de aproximadamente 750 mm (Ruiz-Esparza *et al.* 2012) (**Figs. 6E–H**).

Reserva Biológica Guaribas (Rebio Guaribas), Paraíba

Constitui um dos últimos remanescentes de Floresta Atlântica do Estado da Paraíba abrigando espécies animais e vegetais raras, endêmicas e ameaçadas de extinção, colabora com a conservação da diversidade biológica, localizando-se a aproximadamente 44 km a noroeste da capital estadual, João Pessoa, na mesorregião da Mata Paraibana (IBAMA 2003). A Rebio Guaribas está incluída na área Mamanguape/Baía Formosa (Paraíba/Rio Grande do Norte), sendo realizada coleta na área de Mamanguape (6°40'–6°46'S e 35°07'–35°12'W) (Aguiar & Martins 2002) (**Figs. 7A–D**).

Parque Nacional Serra de Itabaiana, Sergipe

Possui 7966 ha, é constituído por um conjunto de serras residuais que compõem um Domo, as quais se destacam as serras de Itabaiana, Cajueiro e Comprida, está localizado na microrregião do agreste apresentando altitudes variando de 400 e 659 m e é considerada pelo Ministério do Meio Ambiente como de alta importância para a conservação da biodiversidade (Sobral *et al.* 2007) (**Figs. 7E–H**).

Parque Nacional do Itatiaia (PNI), Rio de Janeiro e Minas Gerais

Está localizada na região Sudeste do Brasil, mais especificamente entre o sudoeste do Estado do Rio de Janeiro e o Sul do de Minas Gerais (22°30'–22°33'S e 42°15'–42°19'W), na Serra da Mantiqueira, abrangendo área de cerca de 30.000 ha (Mezabarba *et al.* 2013; Simões & Monné 2010). Inserido no Domínio Florestal Atlântico, o PNI possui vegetação classificada como Floresta Ombrófila Densa (Veloso *et al.* 1991) e é considerada a primeira unidade de conservação criada oficialmente no Brasil, em 1937 (Mendes & Padovan 2000) (**Figs. 8A–D**).

Reserva da Una (Rebio Una), Bahia

Localizado no município de Una (15°10' S e 39°03' W), a vegetação da região é essencialmente de Mata Atlântica, caracterizada como uma formação de floresta ombrófila que predomina, em geral, junto aos cordões litorâneos e zonas de baixas altitudes no sul e

sudeste da Bahia (Paciencia & Prado 2004; Nemésio 2013). A maior parte da reserva consiste em florestas secundárias em vários estágios sucessionais, uma vez que pastagens, outras culturas e principalmente plantações de cacau aconteceram na área antes do estabelecimento da reserva em 1979, mas áreas florestais intocadas também podem ser encontradas na REBIO (Nemésio 2013) (**Figs. 8E–H**).

Estação Biológica Santa Lúcia, Espírito Santo

A origem da Estação Biológica Santa Lúcia (EBSL) está vinculada ao trabalho de Augusto Ruschi que fundou o Museu de Biologia Prof. Mello Leitão em 1949 na cidade de Santa Teresa, Espírito Santo (Mendes & Padovan 2000). A EBSLA consiste em um remanescente de Mata Atlântica (19° 57' S e 40° 32' W). Atualmente a área está protegida pela legislação federal pertinente à Mata Atlântica, além de estar inserida na área da Reserva da Biosfera da Mata Atlântica (Mendes & Padovan 2000; Simon 2000). Possui uma área total de aproximadamente 440 ha e considera-se o clima como subtropical úmido, sem estiagem, com temperatura do mês mais quente superior a 22°C e do mês mais frio entre 3 e 18°C (Mendes & Padovan 2000; Simon 2000) (**Figs. 9A–D**).

Floresta Nacional do Amapá, Amapá

A Floresta Nacional do Amapá está localizada nos municípios de Amapá, Ferreira Gomes e Pracuúba (51° 53' 37" W e 01° 06' 37" N) (Pereira *et al.* 2007). Considerada uma Unidade de Conservação Federal criada pelo Decreto nº. 97.630 de 10 de abril de 1989, abrange uma área de 412.000 ha (Brandão & Silva 2008). A área é formada por florestas tropicais ombrófilas densas, dos tipos: Floresta Densa de Terra Firme, que se apresenta na forma de grandes maciços florestais recobrimdo extensas áreas fortemente colinosas e em menores proporções, de Floresta de várzea, que constitui a vegetação típica das margens dos rios que entrecortam a unidade de conservação e das baixadas alagadas no interior da área (Brandão & Silva 2008; Drummond *et al.* 2008) (**Figs. 9E–H**).

Parque Estadual do Acaraí, Santa Catarina

O Parque Estadual de Acaraí foi instituído pelo Decreto nº 3.517, em 23 de setembro de 2005. Situado no litoral norte do Estado de Santa Catarina, no município de São Francisco do Sul, Santa Catarina, 26°19'14.0"S, 48°33'13.0"W, ca. 10 m, possui uma área de aproximadamente 6.667 ha, abrangendo a restinga da Praia Grande e todo o complexo

hidrológico do rio Acaraí, nascentes do rio Perequê e lagoa do Capivaru (Vitali & Uhlig 2009; Xavier-Leite *et al.* 2018).

Reserva Extrativista do Rio Cajari, Amapá

O Resex do rio Cajari, possui uma área de 501.771 ha que abrange três municípios - Laranjal do Jarí, Mazagão e Vitória do Jari. Criada por meio do Decreto nº 9.145 de 12 de março de 1990, hoje categorizada como uma Unidade de Conservação de Uso Sustentável e situada no sul do estado do Amapá (Souza 2006).

RPPN Fazenda São Pedro, Alagoas

Localizada no estado de Alagoas, município de Pilar, a RPPN Fazenda São Pedro localiza-se a 24 km de São Miguel dos Campos (Sergipe) e 50 km de Maceió, na estrada BR 101, 09° 37'S e 35° 58'W, 50 m; considerada remanescente de Mata Atlântica (Cáceres 2007).

Reserva Florestal Adolpho Duke, Amazônia Central

Localizada no município de Manaus, Amazonas, a Reserva Florestal Adolpho Duke é considerada uma unidade de conservação de floresta primária conservada e um ecossistema de terra-firme, área localizada em baixio, entre as coordenadas 59°52'40" e 59°58'00" de longitude Oeste e 03°00'00" e 03°08'00" de latitude Sul (Alencar 1994; Ruiz & Alencar 2004; Cáceres & Aptroot 2017).

○ **América Latina**

As demais coletas foram realizadas na Guatemala, mais precisamente nas áreas do Biotopo del Quetzal, Purulhá, Baja Verapaz; Quiriguá; e Tikal (Barillas & Lücking 1992; Barillas *et al.* 1993; Lücking 2008b). Na Costa Rica, as coletas foram realizadas em Altamira, na Floresta Tropical Montanhosa em Monteverde, em Orossi e na Floresta Neotropical, na Estação Biológica La Selva (Lücking 1997b, 1999a, c).

Para o Panamá, os líquens foliícolas foram coletados em Barro Colorado Island, e em Cuba, no Parque Nacional Viñales, uma área protegida próxima à província cubana de Piñar del Río (Oliva-Oliveira & Real 2009).



Figura 5: Áreas de coletas de líquens foliícolas da família Gomphillaceae representando o Brejo de Altitude. **A–D.** O Parque Estadual Mata do Pau-Ferro, localizado no estado da Paraíba, Nordeste, Brasil. **E–H.** A Serra da Jiboia, localizada no estado da Bahia, Nordeste, Brasil.



Figura 6: Áreas de coleta de representantes da família Gomphillaceae no Nordeste brasileiro e consideradas áreas de Brejo de Altitude, localizadas no Bioma Caatinga. **A–D.** O Parque Ecológico Municipal João Vasconcelos Sobrinho, mais conhecido por Brejo dos Cavalos, localiza-se no estado de Pernambuco, Brasil. **E–H.** A Serra da Guia, localizada no estado de Sergipe, mais precisamente no município de Poço Redondo.

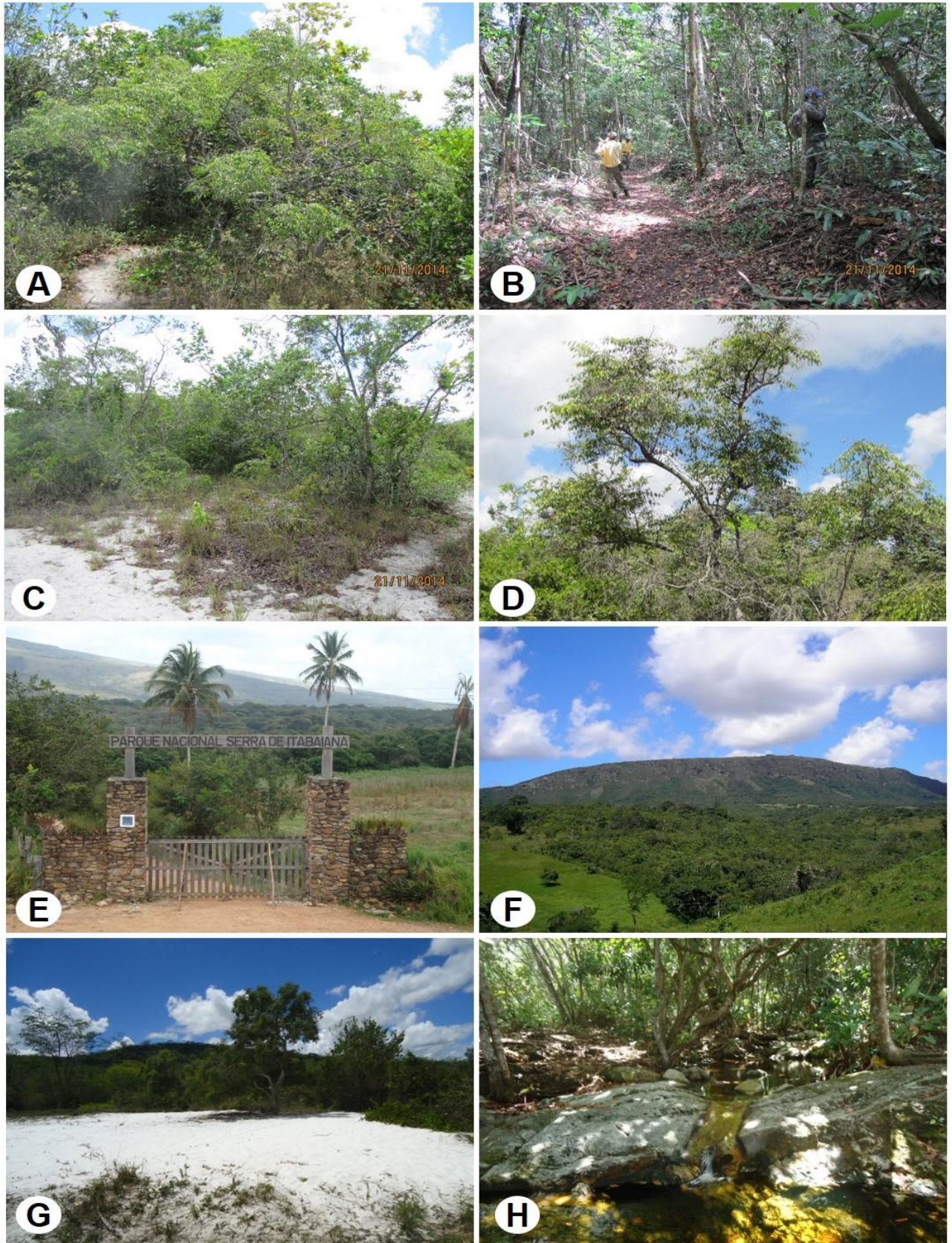


Figura 7: Áreas de Mata Atlântica no Nordeste brasileiro, onde amostras de líquens foliícolas da família Gomphillaceae foram coletadas. **A–D.** Reserva Biológica Guaribas (Rebio Guaribas), localizado no estado da Paraíba. **E–H.** O Parque Nacional Serra de Itabaiana, localizado no estado de Sergipe.



Figura 8: Unidades de Conservação que representam áreas de Mata Atlântica em que coletas foram realizadas durante a pesquisa de líquens da família Gomphillaceae. **A–D.** Parque Nacional do Itatiaia (PNI), localizado na região Sudeste do Brasil. **E–H.** Reserva Biológica de Una (Rebio Una), localizado no estado da Bahia, Nordeste do Brasil.



Figura 9: Áreas de coletas de líquens foliícolas. **A–D.** A Estação Biológica Santa Lúcia, localiza-se no estado do Espírito Santo e representa a Mata Atlântica no Sudeste do Brasil. **E–H.** A Floresta Nacional do Amapá ou FLONA do Amapá, encontra-se no estado do Amapá, região Norte, e representa a Amazônia brasileira.

3.2 Coleta de dados

Para a amostragem do material, foi realizada uma expedição para cada área de estudo, usando a técnica de coleta oportunista (Cáceres *et al.* 2008; Sipman *et al.* 1996). Este método consiste na coleta em árvores selecionadas ao longo das principais trilhas dentro dos fragmentos da floresta, bem como penetrar na vegetação, quando possível. As árvores selecionadas foram abordadas de forma aleatória e com base na seleção visual através da presença de líquens foliícolas, e cada árvore foi inspecionada por cerca de 3-5 min (Cáceres *et al.* 2008).

Esta metodologia garante a coleta de material diversificado e em bom estado para identificação e análises moleculares. Geralmente, uma única folha de tamanho médio pode conter mais de 100 indivíduos de líquens e de 05-50 espécies diferentes podem ser encontradas (Farkas & Sipman 1993), das quais entre 10% e 70% podem ser da família Gomphillaceae. Assim, a coleta de 100 folhas por localidade poderia resultar facilmente em milhares de amostras, das quais se pode fazer uma seleção para estudar as melhores de cada espécie.

3.3 Processamento e identificação das amostras líquênicas

Ainda em campo, o material coletado foi secado com auxílio de prensas botânicas utilizando jornais e papelão em temperatura ambiente. Em laboratório, as amostras foram guardadas em envelopes maiores de papel branco A4 com etiquetas do Herbário ISE, campus Professor Alberto Carvalho, Itabaiana, contendo características do local de coleta (unidade de conservação, Município, coordenadas geográficas, altitude, bioma), e em seguida, colocadas no freezer organizados em caixas plásticas. As amostras foram armazenadas em freezer no Laboratório de Biologia de Micorrizas, Universidade Federal do Rio Grande do Norte, e no Laboratório de Líquens, Universidade Federal de Sergipe.

A triagem do material somada à identificação foi realizada no *Botanischer Garden und Botanisches Museum (BGBM)* em Berlin, Alemanha, sob a orientação do Dr. Robert Lücking, coorientador e especialista da área. Previamente à identificação, foram feitas fotos das folhas e etiquetas (**Figs. 10A–B**). Essas fotos foram organizadas, junto com a etiqueta, em *PowerPoint* para que pudesse ser feita a triagem dos gêneros presentes. Para a identificação das espécies foram feitos cortes histoquímicos para visualizar ascósporos, hifóforos, além da análise morfológica dos apotécios utilizando lupa LEICA Zoom 2000 e microscópio ZEISS Axioscope (**Fig. 10C**). Para as fotos individuais de talos e ascomas foi utilizada câmera Sony Cyber-shot DSC-H90 16.1 MP aproximando e focando junto às lentes do microscópio e lupa.

Depois de confirmada a espécie, todas as características observadas foram colocadas em uma tabela no formato Excel. Quando as amostras se repetem, não se faz necessário tirar fotos.

Para análise molecular, foram selecionadas quantidades significativas de amostras que representassem todos os gêneros da família para que obtivéssemos uma árvore filogenética mais completa possível. Dessa forma, fragmentos dos ascomas e/ou hifóforos, foram retirados da folha cuidadosamente para que não houvesse contato com a superfície da folha com o auxílio de bisturi e pinça previamente limpos com álcool 70%, recolhidos em tubos tipo Eppendorf de 1,5 ml e armazenados em freezer (-20°C) até a extração do DNA. Cada eppendorf foi marcado com o número correspondente ao código utilizado para extração molecular (**Fig. 10D**).

Foi usada a monografia de Lücking (2008b), sobre os líquens foliícolas neotropicais, em combinação com os guias coloridos publicados sobre a família Gomphillaceae [http://emuweb.fieldmuseum.org/botany/rlg/search_rlg.php] para identificação dos gêneros e as espécies, como também, chaves provenientes de artigos publicados sobre o grupo, como Lücking *et al.* (2006) para o gênero *Gyalideopsis*.

3.4 Extração, Purificação e Sequenciamento das amostras

O DNA foi extraído utilizando o kit de extração de DNA e PCR para tecidos vegetais da marca Sigma (Sigma-Aldrich REDEExtract-N-Amp Plant PCR Kit – (St. Louis, Missouri, U.S.A.), seguindo instruções do fabricante.

O sucesso da extração foi verificado através de eletroforese em gel de agarose (1,5%) e a qualidade do DNA foi avaliada por espectrofotometria. O DNA foi armazenado em freezer (-20°C) até seu uso em reações de PCR (**Figs. 10E–F**). Os primers utilizados para mtSSU foram: mr-SSU1 (Zoller *et al.* 1999) e MSU7 (Zhou & Stanosz 2001), e para nuLSU: LR0R (Cubeta *et al.* 1991) e LR3 (Vilgalys & Hester 1990), que tem demonstrado serem bons primers específicos para fungos, mais precisamente para trabalhos realizados com a família Gomphillaceae (Lücking *et al.* 2004). Os parâmetros de ciclagem da reação para PCR de mtSSU foi 94 °C 10 min, 94 °C 45 s, 50 °C 45 s, 72 °C 1 min 30 s, em seguida 35 ciclos de 94 °C 45 s, 72 °C 10 min. E para o nuLSU, 95 °C 3 min, 95 °C 45 s, 54 °C 45 s, 72 °C 1 min, em seguida 35 ciclos de 95 °C 45 s, 72 °C 10 min.

O resultado da amplificação foi verificado por eletroforese em gel de agarose 1,5% e os produtos de amplificação foram purificados utilizando o EXOSAP – IT PCR Clean – up e enviados para sequenciamento na Macrogen Europe, Amsterdam, Netherlands [<https://dna.macrogen.com/eng/>] (**Figs. 10G–H**).

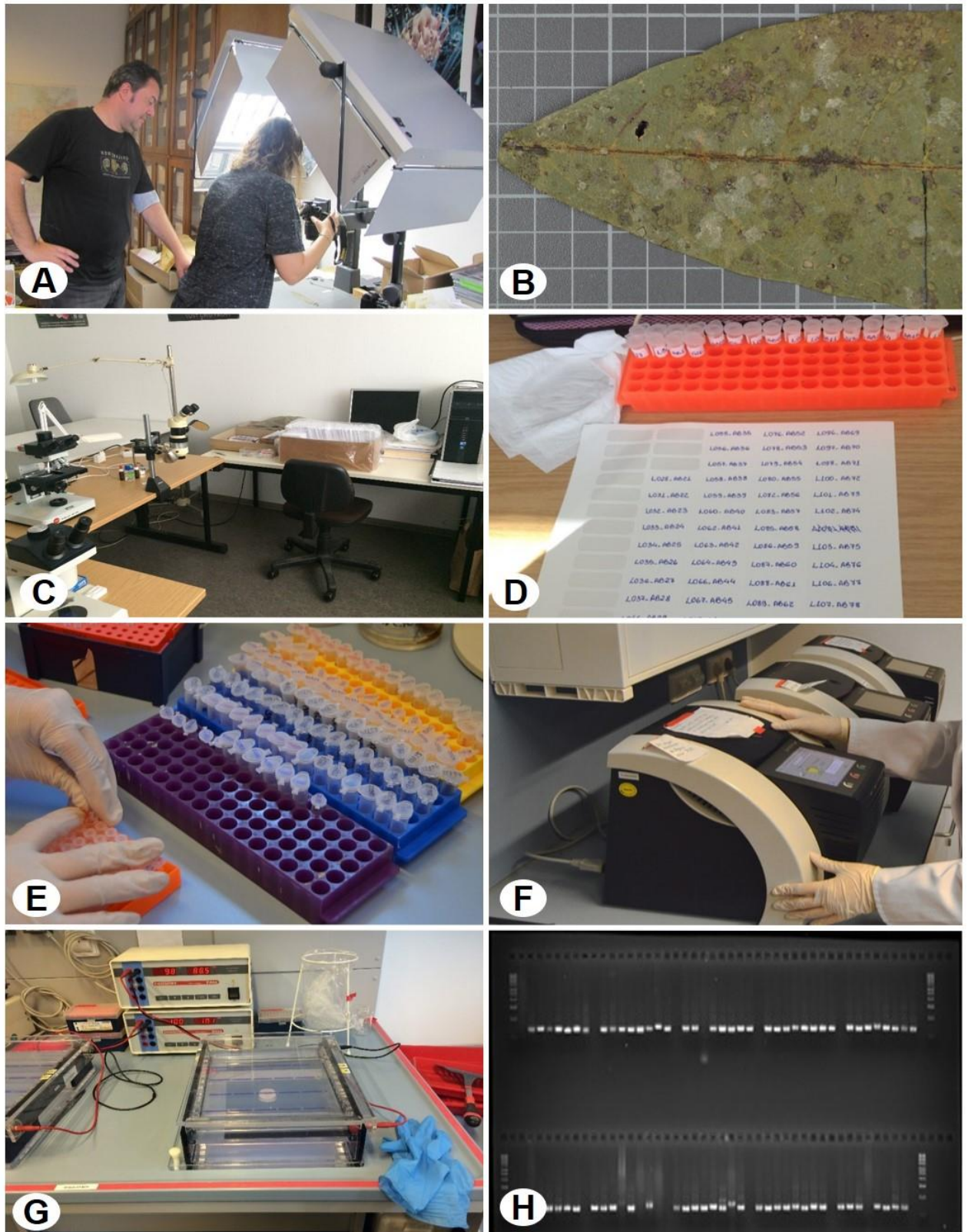


Figura 10: Análises morfológica e molecular dos espécimes selecionados no *BGBM*, Berlin, Alemanha. **A - B.** Fotos das etiquetas, folhas e espécimes selecionados. **C.** Sala devidamente estruturada para análise morfológica e microscópica. **D.** Confecção de etiquetas para análise molecular. **E–F.** Tubos de eppendorfs preparados para extração de DNA e amplificação por PCR. **G–H.** Eletroforese em gel de agarose e resultado das bandas dos produtos da PCR.

3.5 Alinhamento das sequências e análises filogenéticas

As sequências obtidas foram alinhadas com outras baixadas do GenBank com o auxílio do programa MAFFT 7 (Katoh *et al.* 2009, Katoh 2013) e editadas usando o programa BioEdit 7.2.0 (Hall 1999). A caracterização molecular final se deu com a avaliação filogenética e construção de árvores usando verossimilhança máxima (VM), realizada com o programa RAxML 8.2.0 (Stamatakis 2006, 2014), usando o modelo geral reversível GTR com 1000 repetições de bootstrap.

4. RESULTADOS

Como resultado das coletas nas áreas selecionadas, 2.123 folhas foram triadas e analisadas de acordo com a presença de líquens foliícolas pertencentes a família Gomphillaceae.

Destas, 503 espécimes foram identificados e selecionados para extração molecular, totalizando 1.754 sequências enviadas para sequenciamento, sendo 820 sequências de mtSSU e 934 sequências de nuLSU. Porém, levando em consideração as sequências não contaminadas, 335 espécimes de líquens foliícolas foram utilizados nas análises moleculares representando 464 sequências que geraram a árvore final da família Gomphillaceae, sendo 109 para o Brejo de Altitude, 101 para Mata Atlântica, 54 para Amazônia, 44 para a América Latina, 28 sequências foram extraídas do GenBank (incluindo *outgroup*) e uma doada pelo Dr. André Aptroot.

Quanto às sequências, 272 são novas sequências de nuLSU e 136 de mtSSU para a família Gomphillaceae, alinhadas com 29 sequências de mtSSU e 27 sequências de nuLSU rDNA extraídas do Genbank.

Diante dos dados apresentados, a tese está composta de quatro capítulos no formato de artigos científicos em inglês que serão submetidos em periódicos internacionais, como *Lichenologist* e *Fungal Diversity*:

- ✓ **Capítulo 01** - A phylogenetic revision of the classification of the lichenized family Gomphillaceae (Ascomycota: Ostropales);
- ✓ **Capítulo 02** - New genera in the lichenized family Gomphillaceae (Ascomycota: Ostropales) utilizing Integrative Taxonomy;
- ✓ **Capítulo 03** - Reclassification of species in the lichenized family Gomphillaceae (Ascomycota: Ostropales) using morphology-based phylogenetic binning;

- ✓ **Capítulo 04** - The genus *Gyalideopsis* (lichenized Ascomycota: Gomphillaceae) in Brazil: updated checklist, key to species, and two novel taxa with unique hyphophores (publicado em: *The Bryologist* 121(1): 32-40, 2018).

5. CONCLUSÕES GERAIS

Diante dos resultados do presente trabalho, a família Gomphillaceae é considerada atualmente a mais diversa família de líquens foliícolas. A família que consistia de 25 gêneros, agora dispõe de 42 gêneros devido às análises filogenéticas somadas às análises taxonômicas, que permitiram atualizar a classificação filogenética da família com a descoberta e descrição de 13 novos gêneros, 4 gêneros restabelecidos, bem como, 53 novas combinações.

Como esperado, as combinações das principais características fenotípicas para a família Gomphillaceae, como talo, apotécio e hifóforos, denotam linhagens a nível de gênero na família, fornecendo uma sistemática mais robusta e permitindo avaliar relações filogenéticas e evolutivas entre gêneros e relações evolutivas entre esses principais tipos de morfologia de ascomas e hifóforos dentro da família Gomphillaceae.

Os resultados ressaltaram a necessidade do aumento de amostragem de táxons, especialmente não-foliícolas, não utilizados nas análises, e adição de pelo menos um marcador de codificação de proteína para aumentar a resolução do *backbone* a fim de permitir uma classificação mais completa dentro da família e poder abordar questões evolutivas mais amplas.

Além do uso da ferramenta *phylogenetic binning* em grupos taxonômicos altamente diversificados e complexos ter demonstrado ser altamente importante para a nova classificação da família, já que dados de sequência em nível taxonômico amplo são muitas vezes ausentes.

5. REFERENCES

- Aguiar, A.J.C., Martins, C.F. 2002. Abelhas e vespas solitárias em ninhos-armadilha na Reserva Biológica Guaribas (Mamanguape, Paraíba, Brasil). *Revista Brasileira de Zoologia* 19(1): 101-116.
- Ahmadjian, V. 1965. *Lichens*. Annual Review of Microbiology 19: 1-20.

- Alencar, J.C. 1994. Fenologia de cinco espécies arbóreas tropicais de Sapotaceae correlacionada a variáveis climáticas na Reserva Ducke, Manaus. *Acta Amazonica* 24(3/4): 161-182.
- Andrade, L.A., Oliveira, F.X., Nascimento, I.S., Fabricante, J.R., Sampaio, E.V.S.B., Barbosa, M.R.V. 2006. Análise florística e estrutural de matas ciliares ocorrentes em brejo de altitude no município de Areia, Paraíba: *Revista Brasileira de Ciências Agrárias* 1: 31-40.
- Aptroot, A., Cáceres, M.E.S. 2013. Pyrenocarpous lichens (except *Trypetheliaceae*) in Rondônia. *The Lichenologist* 45(6): 763-785.
- Baloch, E., Lücking, R., Lumbsch, H.T., Wedin, M. 2010. Major clades and phylogenetic relationships between lichenized and non-lichenized lineages in Ostropales (Ascomycota: Lecanoromycetes). *Taxon* 59: 1483-1494.
- Barbosa, M.R.V., Lima, R.B., Agra, M.F., Cunha, J.P., Pessoa, M.C.R. 2005. Vegetação e flora fanerogâmica do Curimataú, Paraíba. In: Araújo, F.S., Rodal, M.J.N., Barbosa, M.R.V. (eds.) Análise das variações da biodiversidade do bioma Caatinga: suporte a estratégias regionais de conservação. Brasília, Ministério do Meio Ambiente. p. 121-128.
- Barillas, R., Lücking, R. 1992. Líquenes foliícolas de Guatemala. Un estudio taxonómico preliminar. *Cryptogamie, Bryologie-Lichénologie* 13(4): 297-317.
- Barillas, R., Lücking, R., Winkler, S. 1993. Vergesellschaftungen foliikoler Flechten im Biotopo del Quetzal, Guatemala. *Cryptogamie, Bryologie-Lichénologie* 14(1): 49-68.
- Brandão, F.C., Silva, L.M.A. 2008. Conhecimento ecológico tradicional dos Pescadores da Floresta Nacional do Amapá. *UAKARI* 4(2): 55-66.
- Cáceres, M. E. S. 1999. Líquens foliícolas da Mata Atlântica de Pernambuco (Brasil): Diversidade, ecogeografia e conservação. M.S. Thesis, Centro de Ciências Biológicas da Universidade Federal de Pernambuco, Recife, Brazil.
- Cáceres, M.E.S., Lücking, R. 1999. Three new species and one new combination of foliicolous lichens and lichenicolous fungi from the Atlantic rain forest in Pernambuco state, Brazil. *Nova Hedwigia* 70: 217–226.
- Cáceres, M.E.S., Lücking, R. 2006. Diversidade, Biogeografia, Ecologia e Utilização de Líquens Foliícolas. In: Lauro Xavier Filho; Maria Estrella Legaz; Carlos Vicente Cordoba; Eugênia Cristina Pereira. (Org.). *Biologia de Líquens*. 1ed. Rio de Janeiro: Âmbito Cultural Edições Ltda. 1: 521-535.

- Cáceres, M.E.S. 2007. Corticolous crustose and microfoliose lichens of northeastern Brazil. *Libri Botanici* 22: 1-168.
- Cáceres, M.E.S., Lücking, R., Rambold, G. 2008. Corticolous microlichens in northeastern Brazil: habitat differentiation between coastal Mata Atlântica, Caatinga and Brejos de Altitude. *The Bryologist* 111: 98-117.
- Cáceres, M.E.S., Aptroot, A. 2017. Lichens from the Brazilian Amazon, with special reference to the genus *Astrothelium*. *The Bryologist* 120(2): 166- 182.
- Carlile, M.J., Watkinson, S.C., Gooday, G.W. 2001. *The Fungi*. 2nd edition, 76 p.
- Chaparro, M.V., Ceballos, J.A. 2002. *Hongos liquenizados*. Universidad Nacional de Colombia, Sede Bogotá. 1rd edition, 9-12p.
- Cubeta, M.A., Echandi, E., Abernethy, T., Vilgalys, R. 1991. Characterization of anastomosis groups of binucleate *Rhizoctonia* species using restriction analysis of na amplified ribosomal RNA gene. *Phytopathology* 81: 1395-400.
- Deacon, J.W. 2006. *Fungal Biology*. 4ed. Rev. Ed. Of: Modern mycology 268p.
- DeBolt, A.M., Rosentreter, R., Martin, E.P. 2007. Macrolichen diversity in subtropical forests of north-central Florida. *The Bryologist* 110(2): 254–265.
- Drummond, J.A., Dias, T.C.A.C., Brito, D.M.C. 2008. Atlas das unidades de conservação do Estado do Amapá. Macapá: MMA/IBAMA – AP; GEA/SEMA, 128p.
- Etayo, J., Lücking, R. 1999. *Anisomeridium musaesporoides*, a new foliicolous lichen from tropical america. *Lichenologist* 31(2): 145–148.
- Etayo, J. 2017. Hongos Liquenícolas de Ecuador. *Opera Lilloana* 50: 339.
- Farkas, E.E., Sipman, H.J.M. 1993. Bibliography and checklist of foliicolous lichenized fungi up to 1992. *Tropical Bryology* 7: 93–148.
- Farkas, E., Flakus, A. 2012. *Calopadia erythrocephala*, a new foliicolous lichenized fungus from Brazil. *The Lichenologist*, 44(3): 395-399.
- Ferraro, L.I., Lücking, R., Sérusiaux, E. 2001. A world monograph of the lichen genus *Gyalectidium* (Gomphillaceae). *Botanical Journal of the Linnean Society* 137: 311-345.
- Ferraro, L.I., Lücking, R. 2003. *Gyalectidium aurelii* (Ostropales: Gomphillaceae), a new foliicolous lichen from the state of Mato Grosso, Brazil. *Acta Botanica Brasilica* 17(4): 619-622.
- Ferraro, L.I., Lücking, R. 2005. The Genus *Gomphillus* (Ostropales: Gomphillaceae) in the Americas, with the New Species *Gomphillus pedersenii* from Argentina. *The Bryologist* 108: 491-496.

- Feuerer, T., Hawksworth, D.L. 2007. Biodiversity of lichens, including a world-wide analysis of checklist data based on Takhtajan's floristic regions. *Biodiversity Conservation* 16: 85–98.
- Gardes, M., Bruns, T.D. 1993. ITS primers with enhanced specificity for basidiomycetes: application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2: 113–118.
- Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Hawksworth, D., Lücking, R. 2017. Fungal diversity revisited: 2.2 to 3.8 million species. *Microbiology Spectrum* 5(4): 1–17.
- Herrera-Campos, M.A., Lücking, R. 2002. The foliicolous lichen flora of Mexico. I. New species from Los Tuxtlas Tropical Biological Station, Veracruz. - *Lichenologist* 34: 211–222.
- Herrera-Campos, M.A., Lücking, R. 2003. The Foliicolous Lichen Flora of Mexico II. New Species from the Montane Forest in Oaxaca and Puebla. *The Bryologist* 106: 1–8.
- Herrera-Campos, M.A., Lücking, R., Pérez, R.E., Campos, A., Cólín, P.M., Peñã, A.B. 2004. The foliicolous lichen flora of Mexico. V. Biogeographical affinities, altitudinal preferences, and an updated checklist of 293 species. *The Lichenologist* 36: 309–327.
- Herrera-Campos, M.A., Lücking, R., Pérez, R.E., Campos, A., Cólín, P.M., Peñã, A.B. 2004. The foliicolous lichen flora of Mexico. V. Biogeographical affinities, altitudinal preferences, and an updated checklist of 293 species. *The Lichenologist* 36: 309–327.
- Jaklitsch, W.M., Baral, H.O., Lücking, R., Lumbsch, H.T. 2016. Ascomycota. In: Frey, W. (ed.) Syllabus of Plant Families –Adolf Engler's Syllabus der Pflanzenfamilien. Borntraeger, Stuttgart, 288 pp. Kirk, P., Cannon, P.F., Minter, D.W., Stalpers, J.A. 2008. *Ainsworth & Bisby's Dictionary of the Fungi*. Centre for Agricultural Bioscience International, Wallingford, UK.
- Kalb, K., Vězda, A. 1988. Neue oder bemerkenswerte Arten der Flechtenfamilie Gomphillaceae in der Neotropis. *Bibliotheca Lichenologica* 29: 49
- Katoh, K., Asimenos, G., Toh, H. 2009. *Multiple Alignment of DNA Sequences with MAFFT*. In: Posada, D. (ed.) Bioinformatics for DNA Sequence Analysis. *Methods in Molecular Biology* 537: 39–64.
- Katoh, S. 2013. MAFFT: multiple sequence alignment software version 7: improvements in performance and usability (outlines version 7). *Molecular Biology and Evolution* 30: 772–780.

- Kirk, P., Cannon, P.F., Minter, D.W., Stalpers, J.A. 2008. *Ainsworth & Bisby's Dictionary of the Fungi*. Centre for Agricultural Bioscience International, Wallingford, UK.
- Lücking, R. 1991. Neue Arten foliikoler Flechten aus Costa Rica, Zentralamerika. *Nova Hedwigia* 52: 267–304.
- Lücking, R. 1992. Foliicolous lichens - A contribution to the knowledge of the lichen flora of Costa Rica, Central America. *Beih. Nova Hedwigia* 104: 1–179.
- Lücking, R. 1997a. Estado actual de las investigaciones sobre líquenes foliícolas en la región Neotropical, con un análisis biogeográfico preliminar. *Tropical Bryology* 13: 87-114.
- Lücking, R. 1997b. Additions and Corrections to the Knowledge of the foliicolous Lichen Flora of Costa Rica. The Family Gomphillaceae. *Bibliotheca Lichenologica*, 65, J. Cramer, Berlin, Stuttgart. 109 pp.
- Lücking, R., E. Sérusiaux, L. C. Maia & E. C. G. Pereira. 1998. A revision of the names of foliicolous lichenized fungi published by Batista and co-workers between 1960 and 1975. *Lichenologist* 30: 121–191.
- Lücking, R., Cáceres, M.E.S., Maia, L.C. 1999. Revisão taxonômica e nomenclatural de líquens foliícolas e respectivos fungos liquenícolas registrados para o estado de Pernambuco, Brasil, por Batista e colaboradores. *Acta Botanica Brasilica* 13: 115–128.
- Lücking, R. 1999a. Adiciones y correcciones al conocimiento de La liquenoflora foliicola de Costa Rica. La familia Asterothyriaceae y el género Chroodiscus (Thelotremales), con un análisis filogenético. *Cryptogamie Mycologie* 20 (3): 193-224.
- Lücking, R. 1999b. Additions and corrections to the foliicolous lichen flora of Costa Rica. The family Gyalectaceae. *Lichenologist* 31(4): 359–374.
- Lücking, R. 1999c. Líquenes foliícolas de la Estación Biológica La Selva, Costa Rica: Inventario, comunidades y comparación florística de tipos de vegetación. *Revista de Biología Tropical* 47(3): 287-308.
- Lücking, R., Cáceres, M.S., Maia, L.C. 1999a. Revisão nomenclatural e taxonômica de líquens foliícolas e respectivos fungos liquenícolas registrados para o Estado de Pernambuco, Brasil, por Batista e colaboradores. *Acta Botanica Brasilica* 13(2): 115-128.
- Lücking, R., Cáceres, M.E.S., Maia, L.C. 1999b. Catálogo e revisão taxonômica de fungos liquenizados foliícolas, registrados para o estado de Pernambuco (Brasil), por Batista e colaboradores. Departamento de Micologia, Universidade Federal de Pernambuco, Recife, Brazil

- Lücking, R., Kalb, K. 2000. Foliikole Flechten aus Brasilien (vornehmlich Amazonien), inklusive einer Checkliste und Bemerkungen zu *Coenogonium* und *Dimerella* (*Gyalectaceae*) [Foliicolous lichens from Brazil (mainly Amazonia), including a checklist and notes on *Coenogonium* and *Dimerella* (*Gyalectaceae*)]. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 122: 1-61.
- Lücking, R., Farkas, E., Sérusiaux, E., Sipman, H.J.M. 2000a. Checklist of foliicolous lichens and their lichenicolous fungi. Part I. Foliicolous lichens. [<http://www.uni-bayreuth.de/departments/planta2/ass/robert/lichens/checkfol.html>].
- Lücking, R., Diederich, P., Etayo, J. 2000b. Checklist of foliicolous lichens and their lichenicolous fungi. Part II. Lichenicolous fungi. [<http://www.uni-bayreuth.de/departments/planta2/ass/robert/lichens/checkfun.htm>].
- Lücking, R., Sérusiaux, H.J.M., Sipman, H.J.M. 2000. New species or interesting records of foliicolous lichens VII. *Calenia flava* (Ostropales: Gomphillaceae). *Tropical Bryology* 19: 55-58.
- Lücking, R. 2001. Lichens on leaves in tropical rainforests: life in a permanently ephemeral environment. *Dissertationes Botanicae* 346: 41-77.
- Lücking, R., Matzer, M. 2001. High foliicolous lichen alphas diversity on individual leaves in Costa Rica and Amazonian Ecuador. *Biodiversity. Conservation*. 10: 2139-2152.
- Lücking, R., Cáceres, M.E.S. 2002. Liquens foliícolas: diversidade, taxonomia e biogeografia. In Caxiuana: Populações tradicionais, meio físico & diversidade biológica (P.L.B. Lisboa, ed.). *Museu Paraense Emílio Goeldi*, Belém, p. 445- 472.
- Lücking, R., Kalb, K. 2002. New species and further additions to the foliicolous lichen flora of Kenya (East Africa), including the first lichenicolous *Aulaxina* (Ostropales: Gomphillaceae). *Botanical Journal of the Linnean Society* 139: 171–180.
- Lücking, R., Stuart, B.L., Lumbsch, H.T. 2004. Phylogenetic relationships of Gomphillaceae and Asterothyriaceae: evidence from a combined Bayesian analysis of nuclear and mitochondrial sequences. *Mycologia* 96(2): 283–294.
- Lücking, R., Sérusiaux, E. 2005. *Gomphillus morchelloides* (Ostropales: Gomphillaceae), A New Lichen Species. *The Bryologist* 108(4): 487-490.
- Lücking, R., Sérusiaux, E., Vězda, A. 2005. Phylogeny and systematics of the lichen family Gomphillaceae (Ostropales) inferred from cladistic analysis of phenotype data. *The Lichenologist* 37: 123-170.

- Lücking R., Buck, W.R., Sérusiaux E., Ferraro, L.I. 2005. *Gomphilluscaribaeus* Belongs in the New Genus *Bryogomphus* (Lecanorales: Pilocarpaceae). *The Bryologist* 108(4): 481-486.
- Lücking, R., Cáceres, M.E.S. 2006. Taxonomia e Sistemática dos Líquens Foliícolas. In: Xavier Filho, L., Legaz, M.E., Cordoba, C.V., Pereira, E.C. (Orgs.). *Biologia de Líquens*. 1ed. Rio de Janeiro: Âmbito Cultural Edições Ltda.1: 503-518.
- Lücking, R., Aptroot, A., Umaña, L., Chaves, J.L., Sipman, H.J.M., Nelsen, M.P. 2006. A first assessment of the Ticolichen biodiversity inventory in Costa Rica: the genus *Gyalideopsis* and its segregates (Ostropales: Gomphillaceae), with a world-wide key and name status checklist. *The Lichenologist* 38: 131-160.
- Lücking, R., Buck, W.R., Plata, E.R. 2007. The lichen family Gomphillaceae (Ostropales) in eastern North America, with notes on hyphophore development in *Gomphillus* and *Gyalideopsis*. *The Bryologist* 110: 622-672.
- Lücking, R. 2008a. Foliicolous lichens as model organisms to study tropical rainforest ecology: background, data, and protocols. *Honour of Volkmar WIRTH* 15: 335-362.
- Lücking, R. 2008b. *Foliicolous Lichenized Fungi*. The New York Botanical Garden Press, 873p.
- Lücking, R., Wirth, V., Ahrens, M. 2009. Foliicolous Lichens in the Black Forest, Southwest-Germany. *Carolinea* 67: 23-31.
- 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(4): 361-416.
- Machado, W.J., Prata, A.P.N., Mello, A.A. 2012. Floristic composition in areas of Caatinga and Brejo de Altitude in Sergipe state, Brazil. *Check List* 8(6): 1089-1101.
- Mangold, A., Martin, M.P., Lücking, R., Lumbsch, H.T. 2008. Molecular phylogeny suggests synonymy of Thelotremaaceae within Graphidaceae (Ascomycota: Ostropales). *Taxon* 57: 476-486.
- McCarthy, P.M. 1999. *Pocsia mucronata*, a new foliicolous lichen from lord howe island, Australia. *Lichenologist* 31(2): 141–144.
- Mendes, S.L., Padovan, M.P. 2000. A Estação Biológica de Santa Lúcia, Santa Teresa, Espírito Santo. *Boletim do Museu de Biologia Mello Leitão* (N. Sér.) 11/12: 7-34.
- 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: 302–305.

- IBAMA, 2003. Reserva Biológica Guaribas: Plano de Manejo, Fase 2. Ministério do Meio Ambiente. Brasília, IBAMA, 520p.
- Mezabarba, V., Vianna Filho, M.D.M., Borges, R.A.X., Mansano, V.F. 2013. *Ericaceae* do Parque Nacional do Itatiaia, RJ, Brasil. *Hoehnea* 40(1): 115-130.
- Nash III, T.H. 2008. *Lichen Biology*. Cambridge: Cambridge University Press. 2nd edition, 496p.
- Nemésio, A. 2013. The orchid-bee fauna (Hymenoptera: *Apidae*) of ‘Reserva Biológica de Una’, a hotspot in the Atlantic Forest of southern Bahia, eastern Brazil. *Brazilian Journal of Biology* 73(2): 347-352.
- Oliva-Oliveira, M., Real, R. Moluscos terrestres de las elevaciones cársticas de Viñales, Pinar del Río, Cuba. *Revista de Biología Tropical* 57(3): 589-604
- Oliveira, L.F.C., Edwards, H.G.M., Feo-Manga, J.C., Seaward, M.R.D., Lücking, R. 2002. FT-Raman spectroscopy of three foliicolous lichens from Costa Rican rainforests. *Lichenologist* 34: 259-266.
- Paciencia, M.L.B., Prado, J. 2004. Efeitos de borda sobre a comunidade de pteridófitas na Mata Atlântica da região de Una, sul da Bahia, Brasil. *Revista Brasileira de Botânica* 27(4): 641-653.
- Papong, K., Boonpragob, K., Lücking, R. 2007. New species and new records of foliicolous lichens from Thailand. *The Lichenologist* 39(1): 47–56.
- Pereira, L.A., Sena, K.S., Santos, M.R., Neto, S.V.C. 2007. Aspectos florísticos da FLONA do Amapá e sua importância na conservação da biodiversidade. *Revista Brasileira de Biociências*, Porto Alegre 5(2): 693-695.
- Queiroz, L.P., Sena, T.S.N., Costa, M.J.S.L. 1996. Flora Vascular da Serra da Jibóia, Santa Terezinha – Bahia. I: O Campo Rupestre. *Sitientibus*, Feira de Santana 15: 27-40.
- Rivas-Plata, E., Lücking, R., Lumbsch, H.T. 2012. A new classification for the family Graphidaceae (Ascomycota: Lecanoromycetes: Ostropales). *Fungal Diversity* 52: 107-121.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539-542.
- Ruiz, R.R., Alencar, J.C. 2004. Comportamento fenológico da palmeira patauá (*Oenocarpus bataua*) na reserva florestal Adolpho Ducke, Manaus, Amazonas, Brasil. *Acta Amazonica* 34(4): 553 – 558.

- Ruiz-Esparza, J., Rocha, P. A., Ribeiro, A.S., Ferrari, S. 2012. The birds of the Serra da Guia in the caatinga of northern Sergipe. *Revista Brasileira de Ornitologia* 20(3): 290-301.
- Sanders, W.B., De Los Ríos, A. 2016. Structure of foliicolous thalli of the Gomphillaceae in a south-western Florida lichen community. *The Lichenologist* 48(4): 293–303.
- Santesson, R. 1952. Foliicolous lichens – A revision of the taxonomy of the obligately foliicolous, lichenized fungi. *Symbiosis Botanical Upsala* 12(1): 1 – 590.
- Santos, V.M., Lücking, R., Cáceres, M.E.S. 2017. Líquens foliícolas (Ascomycota) em Brejos de Altitude: novos registros para o Nordeste e para o Brasil. *Iheringia Série Botânica* 71: 367–376.
- Seavey, F., Seavey, J. 2014. Four new species and sixteen new lichen records for North America from Everglades National Park. *The Bryologist* 117(4): 395–404.
- Sérusiaux, E. 1986. The nature and origin of campylidia in lichenized fungi. *Lichenologist* 18: 1-35.
- Sérusiaux, E., De Sloover, J.R. 1986. Taxonomical and ecological observations on foliicolous lichens in northern Argentina, with notes on the hyphophores of Asterothyriaceae. *Veröffentlichungen des Geobotanischen Institutes ETH, Stiftung Rübel, Zürich* 91: 260-292.
- Sipman, H.J.M. 1996. Corticolous lichens. In: Gradstein, S.R., Hietz, P., Lücking, R., Lücking, A., Sipman, H.J.M., Vester, H.F.M., Wolf JHD & Gardette, E. How to sample the epiphytic diversity of tropical rain forests. *Ecotropica* 2: 66-67.
- Simões, M.V.P., Monné, L.M. 2010. Inventário das espécies de Cassidinae (Insecta, Coleoptera, Chrysomelidae) do Parque Nacional do Itatiaia, RJ, Brasil. *Biota Neotropica* 11(4): 215-228.
- Simon, J. E. 2000. Composição da Avifauna da Estação Biológica de Santa Lúcia, Santa Teresa – ES. *Boletim do Museu de Biologia Mello Leitão (N. Sér.)* 11/12: 149-170.
- Sobral, I.S., Santana, R.K.O., Gomes, L.J., Costa, M., Ribeiro, G.T., Santo, J.R. 2007. Avaliação dos impactos ambientais Parque Nacional Serra de Itabaiana – SE. *Caminhos de Geografia Uberlândia* 8: 102-110.
- Souza, Walter Paixão de. 2006. A dinâmica dos sistemas de produção praticados em uma unidade de conservação de uso direto na Amazônia – a Reserva Extrativista do Rio Cajari no Estado do Amapá. 166 f. Dissertação (Mestrado) - Universidade Federal do Pará, Empresa Brasileira de Pesquisa Agropecuária, Belém, 2006. Curso de Mestrado em Agriculturas Familiares e Desenvolvimento Sustentável.

- Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688-2690.
- Tabarelli, M., Santos, A.M.M. 2004. Uma breve descrição sobre a história natural dos Brejos Nordestinos. In: Porto, K.C., Cabral, J.J.P., Tabarelli, M. Brejos de altitude em Pernambuco e Paraíba: história natural, ecologia e conservação. Brasília: Ministério do Meio Ambiente, 17p.
- Thor, G., Vězda, A. 1984. Einige neue oder bemerkenswerte Flechten mit gyalectoiden Apothecien von Nord-Indien und Nepal. *Folia Geobotanica et Phytotaxonomica* 19(1): 71-82.
- Van Den Broeck, D., Lücking, R., Ertz, D. 2014. The foliicolous lichen biota of the Democratic Republic of the Congo, with the description of six new species. *The Lichenologist* 46(2): 141–158.
- Vainio, E. 1890. Étude sur la classification naturelle et la morphologie des lichens du Brésil. I-II. Acta Societatis pro Fauna et Flora Fennica 7.
- Vainio, E. 1896. Lichenes antillarum a W. R. Elliott collecti. *Journal of Botany* 34.
- Vězda, A. 1966. Flechtensystematische Studien IV. Die Gattung *Gyalidea* Lett. *Folia Geobotanica et Phytotaxonomica* 1: 311-340.
- Vězda, A. 1972: Flechtensystematische Studien VII. *Gyalideopsis*, eine neue Flechtengattung. - *Folia Geobotanica et Phytotaxonomica, Praha* 7: 203-215.
- Vězda, A. 1979. Flechtensystematische Studien. XI. Beiträge zur Kenntnis der Familie Asterothyriaceae (Discolichenes). *Folia Geobotanica et Phytotaxonomica, Praha* 14: 43–94.
- Vězda, A. 2003. *Gyalideopsis tuerkii* (lichenisierte Ascomycotina, Gomphillaceae), eine neue Art der Alpen. *Herzogia* 16: 35–40.
- Vězda, A., Poelt, J. 1987. Flechtensystematische Studien. XII. Die Familie Gomphillaceae und ihre Gliederung. *Folia Geobotanica et Phytotaxonomica, Praha* 22: 179–198.
- Valente, E.B., Pôrto, K.C., Bôas-Bastos, S.B.V., Bastos, C.J.P. 2009. Musgos (Bryophyta) de um fragmento de Mata Atlântica na Serra da Jibóia, município de Santa Terezinha, BA, Brasil. *Acta Botanica Brasilica* 23(2): 369-375.
- Veloso, H.P., Rangel Filho, A.L.R., Lima, J.C.A. 1991. *Classificação da vegetação brasileira, adaptada a um sistema universal*. Rio de Janeiro, IBGE, Departamento de Recursos Naturais e Estudos Ambientais.

- Vilgalys, R., Hester, M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* 172: 4238-4246.
- Vitali, M., Uhlig, V.M. 2009. Unidades de Conservação de Santa Catarina. Sustentabilidade em Debate. Disponível em: <http://periodicos.unb.br/index.php/sust/article/view/729/446>.
- Xavier-Leite, A.B., Menezes, A.A., Souto, L.S., Aptroot, A., Lücking, R., Santos, V.M. Cáceres, M.E.S. 2015. Epiphytic microlichens as indicators of phytosociological differentiation between Caatinga and Brejos de Altitude. *Acta Botanica Brasilica* 29(4): 457-466.
- 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): 032–040.
- Zhou, S., Stanosz, G. R. 2001. Primers for amplification of mt SSU rDNA, and a phylogenetic study of *Botryosphaeria* and associated anamorphic fungi. *Mycological Research* 105: 1033-1044.
- Zoller, S., Scheidegger, C., Sperisen, C. 1999. PCR primers for the amplification of mitochondrial small subunit ribosomal DNA of lichen-forming ascomycetes. *Lichenologist* 31: 511-516.
- White, T.J., Bruns, T., Lee, S., Taylor, J. 1990. *Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics*. In: Innis, M.A., Gelfand, D.H., Sninsky, J.J., White, T.J. PCR Protocols: a guide to methods and applications. Academic Press, New York, USA, 315-322p.

Capítulo 1

A phylogenetic revision of the classification of the lichenized family
Gomphillaceae (Ascomycota: Ostropales)

**A phylogenetic revision of the classification of the lichenized family
Gomphillaceae (Ascomycota: Ostropales)**

Amanda Barreto Xavier-Leite^{1,5}, Marcela E. da Silva Cáceres², Bibiana Moncada³, Robert
Lücking⁴ and Bruno Tomio Goto⁵

¹ Programa de Pós-Graduação em Sistemática e Evolução, CB, Universidade Federal do Rio Grande do Norte, Campus Universitário, 59072-970, Natal, RN, Brazil; ² Departamento de Biociências, Universidade Federal de Sergipe, CEP: 49500-000, Itabaiana, Sergipe, Brazil; ³ Universidad Distrital Francisco José de Caldas, Cra. 4 No. 26B-54, Torre de Laboratorios, Herbario, Bogotá, Colombia; ⁴ Botanischer Garten und Botanisches Museum, Freie Universität Berlin, Königin-Luise-Strasse 6–8, 14195 Berlin, Germany; ⁵ Departamento de Botânica e Zoologia, CB, Universidade Federal do Rio Grande do Norte, Campus Universitário, 59072-970, Natal, RN, Brazil

ABSTRACT

A phylogenetic revision of the lichen Gomphillaceae based on 464 sequences of nuclear LSU rDNA and mitochondrial SSU rDNA representing 333 OTUs was reconstructed. The phylogenetic analysis resulted in at least 38 clades corresponding mostly to previously recognized genera, but also several newly recognized lineages. The previously distinguished and supported genera were *Actinoplaca*, *Arthotheliopsis*, *Asterothyrium*, *Aulaxina* s.str, *Bullatina*, *Caleniopsis*, *Gomphillus*, *Gyalectidium*, *Gyalidea*, *Jamesiella*, *Linhartia*, *Psorotheciopsis*, *Rolueckia*, and *Rubrotricha*; in contrast, the genera *Aderkomyces*, *Calenia*, *Echinoplaca*, and *Tricharia* resulted in highly polyphyletic genera. The newly recognized genus-level lineages included: the *Aderkomyces albostrigosus* group (reinstated and validated genus *Spinomyces*), the *A. heterellus* group (reinstated genus *Psathyromyces*), the *A. purulhensis* aggregate (new genus *Roselviria*), the *Aulaxina minuta* aggregate (new genus *Aulaxinella*), the *Calenia monospora* aggregate (new genus *Monocalenia*), the *C. solorinoides* aggregate (new genus *Pseudocalenia*), the *C. triseptata* aggregate (new genus *Caleniella*), the *Echinoplaca leucotrichoides* aggregate (reinstated genus *Sporocybomyces*), the *E. lucernifera* aggregate (new genus *Bezerroplaca*), the *E. marginata* aggregate (new genus *Aptrootidea*), the *E. neotropica* aggregate (new genus *Sipmanidea*), the *E. verrucifera* group (new genus

⁵ Corresponding author's e-mail: amandabxleite@hotmail.com

Verruciplaca), the *Gyalideopsis epithallina* group (new genus *Adelphomyces*), the *G. vulgaris* aggregate (new genus *Vezdamyces*), the *Tricharia farinosa* aggregate (new genus *Serusiauxiella*), the *T. hyalina* complex (new genus *Batistomyces*), and the *T. vainioi* group (reinstated genus *Microxyphiomyces*). Some clades need further analysis and expanded taxon sampling, such as the *Calenia lobulata* group and the *Echinoplaca diffluens* aggregate. Several of the species represented by more than one specimen indicate various levels of cryptic speciation. With the new and reinstated genera being treated in a parallel paper, we conclude that this study substantially improves our understanding of phylogenetic classification within Gomphillaceae, pointing out opportunities for further research, including increased taxon sampling considering the bulk of non-foliicolous species. Furthermore, to use of additional markers to increase backbone resolution, and more detailed studies of widespread taxa to document cryptic speciation, to be able the update species richness in this family.

Keywords. Foliicolous lichen, nuclear LSU rDNA, mitochondrial SSU rDNA, new genera, new combinations

1. INTRODUCTION

The family Gomphillaceae Walt. Watson (Watson 1929) is an important component of tropical lichen communities, but with some species also present in temperate regions and was originally based on a single taxon, *Gomphillus calycioides* (Delise ex Duby) Nyl. This taxon usually usually grows on bryophytes and is characterized by elongated apothecia with very long asci and filiform ascospores (Lücking *et al.* 2004, 2005).

Much later, nine additional genera previously treated in other families or newly described were assigned to Gomphillaceae by Vězda & Poelt (1987), namely *Actinoplaca* Müll. Arg., *Aulaxina* Fée, *Calenia* Müll. Arg., *Bullatina* Vězda & Poelt, *Caleniopsis* Vězda & Poelt, *Echinoplaca* Fée, *Gyalectidium* Müll. Arg., *Gyalideopsis* Vězda, and *Tricharia* Fée. Based on a more recent cladistic analysis (Lücking *et al.* 2005), further ten genera were recognized for a total of 19 (with *Bullatina* considered a synonym of *Calenia*), namely *Aderkomyces* Bat., *Aplanocalenia* Lücking, Sérus. & Vězda, *Arthotheliopsis* Vain., *Diploschistella* Vain., *Ferraroa* Lücking, Sérus. & Vězda, *Lithogyalideopsis* Lücking, Sérus. & Vězda, *Hippocrepidea* Sérus., *Jamesiella* Lücking, Sérus. & Vězda, *Paratracharia* Lücking, and *Rubrotricha* Lücking, Sérus. & Vězda.

In the most recent classification of the family, the number of genera increased to 24, with about 418 species, adding two new genera and four genera previously placed in Asterothyriaceae and Solorinellaceae, respectively: *Asterothyrium* Müll Arg., *Gyalidea* Lettau ex Vězda, *Linhartia* Sacc. & P. Syd., *Phyllogyalidea* Lücking & Aptroot, *Psorotheciopsis* Rehm, and *Rolueckia* Papong, Thammath. & Boonpr. (Lücking *et al.* 2017).

Members of Gomphillaceae present great morphological diversity and an ecological amplitude and are mainly distinguished by their thallus, apothecial and hyphophore features (Vězda & Poelt 1987; Lücking 1997, 2008; Lücking *et al.* 2004, 2005). At family level, Gomphillaceae is characterized by its apothecial anatomy, with thin, mostly anastomosing paraphyses, non-amyloid asci with a downwardly projecting ring structure, and mostly thin-walled, hyaline, transversely septate to muriform ascospores (Lücking *et al.* 2007). The photobiont in the family is a green, chlorococcoid alga belonging to the genus *Heveochlorella* (Sanders & De Los Ríos. 2016).

The anamorphic structures first believed to be lichenicolous fungi by Santesson (1952) and later described and illustrated for many foliicolous taxa by Augusto Chaves Batista and his group under separate names were first correctly recognized and characterized by Vězda (1973) as a peculiar type of conidiomata, then termed hyphophores. A typical hyphophore consists of a stipe and a generally apical portion that produces filiform or moniliform conidial chains, the so-called diahyphae. This type of conidioma is a unique synapomorphy in Gomphillaceae (Lücking 2008). This situation is different compared to campylidia, another type of conidiomata common in foliicolous lichens, which are convergent structures found in several unrelated lineages. As a synapomorphy, hyphophores exhibit an morphological variation related to functional adaptations, varying from setiform types to the squamiform hyphophores of *Hippocrepidea* and *Gyalectidium*, as well as the campilidioid structures in *Ferraroa* or the isidioid hyphophores of *Actinoplaca* (Vězda & Poelt 1987; Lücking 1997, 2008; Lücking *et al.* 2004, 2005).

During the 50s and 60s, specimens of Gomphillaceae with hyphophores were described under separate names by the Brazilian mycologist Augusto Chaves Batista and his co-workers (Batista 1961; Batista & Peres 1964; Batista & Maia 1967; Batista & Poroca 1970; Lücking *et al.* 1998, 1999). Since dual nomenclature is not allowed in lichen fungi and from 2012 onwards not in fungi as a whole, Lücking *et al.* (1998, 1999) established most of these names as synonyms of existing genera, such as *Actinoteichus* Cavalc. & Poroca (= *Asterothrium*), *Aderkomyces* Bat. (= *Tricharia*), *Microxyphiomyces* Bat., Valle & Peres (= *Tricharia*), *Phallomyces* Bat. & Valle (= *Echinoplaca*), *Psathyromyces* Bat. & Peres (= *Tricharia*),

Sporocybomyces H. Maia (= *Echinoplaca*), and *Tauromyces* Cavalc. & A.A. Silva (= *Gyalectidium*).

While the internal classification of the lineages now included in Gomphillaceae was initially based on ascoma structure (Santesson 1952), hyphophores and their diahyphae provided a rich set of additional characters to define genera, which was consequently used in various works to refine the genus diagnose in the family (Vězda 1973; Vězda & Poelt 1987; Lücking 1997, 2008), including a thorough cladistic study that recognized several new genera or reinstated previously established names for particular lineages (Lücking *et al.* 2005). The phylogenetic position of Gomphillaceae, on the other hand, was disputed ever since it was first established by Watson (1929), who compared *Gomphillus* with cladonioid lichens. Subsequently, the family was related to lineages in Ostropales or even considered a separate order within ascolocular fungi (Hafellner 1988). The first molecular study on the family confirmed its position within Ostropales (Lücking *et al.* 2004), together with Stictidaceae, Graphidaceae (= Thelotremaaceae), Gyalectaceae, but also suggested that the only sequenced representative of Asterothyriaceae, *Asterothyrium longisporum* Lücking, belonged in Gomphillaceae. Baloch *et al.* (2010) and Rivas Plata *et al.* (2013) suggested that Gomphillaceae may be nested within Graphidaceae, and Gomphillaceae was even classified as subfamily within Graphidaceae in Rivas Plata *et al.* 2012). However, a recent study was able to show that this was the result of a particular, unique artifact of the phylogenetic analysis (Lücking *et al.*, in prep.), and so Gomphillaceae is now again kept separately (Lücking *et al.* 2017).

The present study aimed to review molecular phylogenetic study of the family, considerably expanding the sampling at genus and species level, focusing on foliicolous lineages. The main objectives were: (1) to test the genus classification established by Lücking *et al.* (2005) based on phenotype features; (2) to assess phylogenetic relationships between genera; and (3) to evaluate the evolutionary relationships of the principal types of ascomata and hyphophore morphologies. For selected groups in which specimen sampling was particularly dense, such as in the genera *Gyalectidium* and *Tricharia*, we also attempted to assess current species concepts.

Our results suggest that Gomphillaceae can be divided into 42 genera, delimited by a combination of thallus, apothecial and hyphophore features, and that the genera *Asterothyrium*, *Gyalidea*, *Linhartia*, *Psorotheciopsis* were formerly and variously separated in the families Asterothyriaceae and Solorinellaceae.

2. MATERIALS AND METHODS

2.1 Taxon sampling

Lichens were newly collected by ABXL and MESC from leaves in various areas in Northeastern Brazil and Amazonia. We further added material from recent collections by RL in other areas of the Neotropics, namely Mexico, Guatemala, Costa Rica, Panama, and Cuba (see General Introduction for details on and references to localities).

2.2 Molecular methods

Leaves with foliicolous lichens were carefully dried after collection and stored at -20°C until DNA extraction. Due to their usually small size, which often requires removal of complete specimens, the specimens targeted for DNA extraction were identified and their characters documented, including photographs of the thalli and their features. Pieces of thalli or in many cases entire thalli were then removed and placed in Eppendorf type tubes (1.5 ml). Total genomic DNA was extracted using the Sigma-Aldrich REDExtract-N-Amp Plant PCR Kit (St. Louis, Missouri, U.S.A.), following the manufacturer's instructions but using less amount of reagents.

Extracted DNA was visualized through electrophoresis on a 1.5% agarose gel and the quality of the DNA evaluated by spectrophotometry. The forward primer mr-SSU1, and the reverse primer MSU7 (Zhou & Stanosz 2001) were used to amplify the mitochondrial small subunit rRNA (mtSSU), with the following PCR specifications: initial denaturation for 10 min at 94°C , 45 s at 94°C , 45 s at 50°C , followed by 35 cycles of 45 s at 94°C , 10 min at 72°C . Using the forward primer LR0R (Vilgalys & Hester 1990) and LR3 (Vilgalys & Hester 1990), the nuclear large subunit rRNA (nuLSU) was amplified through PCR as follows: initial denaturation 3 min at 95°C , 45 s at 95°C , 45 s at 54°C , 1 min at 72°C , then 35 cycles of 45 s at 95°C , and a final elongation for 10 min at 72°C . PCR products were purified with ExoSAP-IT™ (IT PCR Clean-up protocol) and sent for sequencing to Macrogen Europe, Amsterdam, Netherlands [<https://dna.macrogen.com/eng/>].

2.3 Sequence alignment

The obtained new sequences were assembled separately for both markers with sequences from GenBank (Table 1) in BioEdit 7.2.0 (Hall 1999), using species of *Fissurina* (Graphidaceae) as outgroup. The mtSSU alignment contained 165 OTUs and the nuLSU alignment 299 OTUs. Alignment lengths were 944 bp for the mtSSU region and 654 bp for the LSU region, with 920 variable sites. Both data sets were automatically aligned using

MAFFT 7.304 (Katoh *et al.* 2009, Katoh 2013). The obtained alignments were manually inspected in BioEdit and introns and ambiguously aligned portions were delimited using the HoT scores approach on the Guidance Web Server [<http://guidance.tau.ac.il>] to assess alignment confidence scores for each site (Penn *et al.* 2010a, b).

2.4 Phylogenetic analysis

Both markers were first separately analysed through a maximum likelihood approach using RAxML 8.2.0 (Stamatakis 2006, 2014), employing the reversible GTR model with 1000 non-parametric bootstrap replicates. After testing for topological conflict, both data sets were concatenated and the combined tree was reconstructed using the same approach.

3. RESULTS

We generated a total of 136 new mitochondrial SSU rDNA and 272 new nuclear LSU rDNA sequences for this study, which were aligned with 29 mtSSU and 27 nuLSU rDNA sequences downloaded from Genbank. The concatenated data set consisted of 464 sequences representing 333 OTUs, with 329 belonging to the ingroup. Of the sequenced OTUs, 264 originated from Brazilian ecosystems being 109 from Caatinga, 101 from Atlantic forest and 54 from the Amazon; 44 further sequences originated from Mexico, Guatemala, Costa Rica, Panama, and Cuba.

Table 1. GenBank accession numbers and voucher information (for newly generated sequences) for the taxa used in this analysis.

Taxon	Country	Collector	Nr.	Extract	mtSSU	nuLSU
<i>Fissurina aggregatula</i>	[outgroup]				JX421036	JX421490
<i>Fissurina astroisidiata</i>	[outgroup]				JX421040	JX421491
<i>Fissurina insidiosa</i>	[outgroup]				DQ972995	DQ973045
<i>Fissurina nigrolabiata</i>	[outgroup]				JF828961	JF828976
<i>Actinoplaca</i> aff. <i>ampullifera</i>	Cuba	Lücking <i>et al.</i>	41877a	22928	XXX	XXX
<i>Actinoplaca</i> aff. <i>strigulacea</i>	Brazil	Xavier-Leite <i>et al.</i>	2722	22143	—	XXX
<i>Actinoplaca</i> aff. <i>strigulacea</i>	unknown				—	DQ782905
<i>Actinoplaca ampullifera</i>	Brazil	Xavier-Leite	1988	22026	XXX	XXX
<i>Actinoplaca strigulacea</i>	Brazil	Xavier-Leite	1568b	23061	—	XXX
<i>Actinoplaca strigulacea</i>	Guatemala	Lücking	4346	22804	XXX	—
<i>Aderkomyces</i> aff. <i>heterellus</i>	Brazil	Cáceres & Aptroot	28673	23163	XXX	XXX
<i>Aderkomyces</i> aff. <i>heterellus</i>	Brazil	Cáceres & Aptroot	28675	23116	XXX	XXX

<i>Aderkomyces albostrigosus</i>	Brazil	Xavier-Leite	1936	22194	—	XXX
<i>Aderkomyces albostrigosus</i> f. <i>aggregatus</i>	Brazil	Xavier-Leite	1966a	22195	—	XXX
<i>Aderkomyces heterellus</i>	Brazil	Xavier-Leite	1977	22077	XXX	XXX
<i>Aderkomyces heterellus</i>	Brazil	Xavier-Leite	1989	22028	XXX	XXX
<i>Aderkomyces heterellus</i>	Brazil	Xavier-Leite	2001	22012	XXX	—
<i>Aderkomyces heterellus</i>	Brazil	Xavier-Leite	2533	22097	XXX	XXX
<i>Aderkomyces heterellus</i>	Brazil	Xavier-Leite	2589	22062	—	XXX
<i>Aderkomyces heterellus</i>	Brazil	Xavier-Leite <i>et al.</i>	2799	22157	XXX	XXX
<i>Aderkomyces heterellus</i>	Brazil	Xavier-Leite <i>et al.</i>	2909	22130	XXX	—
<i>Aderkomyces heterellus</i>	Brazil				KF833342	KF833330
<i>Aderkomyces heterellus</i>	Cuba	Lücking <i>et al.</i>	41882	22939	XXX	—
<i>Aderkomyces papilliferus</i>	Brazil	Xavier-Leite	1904	22191	—	XXX
<i>Aderkomyces purulhensis</i>	Brazil	Xavier-Leite	1950	22008	XXX	XXX
<i>Aderkomyces purulhensis</i>	Brazil	Xavier-Leite	1966b	22196	XXX	XXX
<i>Aderkomyces purulhensis</i>	Brazil	Xavier-Leite	2085a	23104	XXX	XXX
<i>Aderkomyces</i> sp.	Brazil	Xavier-Leite	2004	22016	XXX	XXX
<i>Aderkomyces</i> sp.	Brazil	Xavier-Leite <i>et al.</i>	2773	22102	XXX	—
<i>Aderkomyces</i> sp. nov.	Brazil	Cáceres & Aptroot	28689	23161	—	XXX
<i>Aderkomyces</i> sp. nov.	Brazil	Cáceres & Aptroot	28693	23162	—	XXX
<i>Arthotheliopsis</i> cf. <i>planicarpus</i>	Brazil	Xavier-Leite	1892	22179	—	XXX
<i>Arthotheliopsis</i> cf. <i>planicarpus</i>	Brazil	Xavier-Leite	2495	22055	—	XXX
<i>Arthotheliopsis tricharioides</i>	Brazil	Xavier-Leite	1924	22086	XXX	XXX
<i>Asterothyrium</i> aff. <i>leucophthalmum</i>	Cuba	Lücking <i>et al.</i>	41904	22935	—	XXX
<i>Asterothyrium</i> aff. <i>leucophthalmum</i>	Cuba	Lücking <i>et al.</i>	42062	22936	—	XXX
<i>Asterothyrium</i> aff. <i>microsporum</i>	Guatemala	Lücking	4455	22819	—	XXX
<i>Asterothyrium</i> cf. <i>microsporum</i>	Cuba	Lücking <i>et al.</i>	41885a	22932	—	XXX
<i>Asterothyrium leucophthalmum</i>	Brazil	Xavier-Leite <i>et al.</i>	1092	23083	—	XXX
<i>Asterothyrium leucophthalmum</i>	Brazil	Xavier-Leite <i>et al.</i>	1176	23081	—	XXX
<i>Asterothyrium leucophthalmum</i>	Brazil	Xavier-Leite <i>et al.</i>	1178	23082	—	XXX
<i>Asterothyrium longisporum</i>	Costa Rica				AY341363	AY341349
<i>Asterothyrium microsporum</i>	Brazil	Xavier-Leite	2107	23084	—	XXX
<i>Asterothyrium rotuliforme</i>	Brazil	Xavier-Leite <i>et al.</i>	1098	22161	—	XXX
<i>Asterothyrium rotuliforme</i>	Guatemala	Lücking	4519	22814	—	XXX
<i>Asterothyrium</i> sp.	Cuba	Lücking <i>et al.</i>	41877c	22930	—	XXX
<i>Aulaxina</i> aff. <i>minuta</i> 1	Brazil	Xavier-Leite <i>et al.</i>	1121	23092	—	XXX
<i>Aulaxina</i> aff. <i>minuta</i> 1	Brazil	Xavier-Leite <i>et al.</i>	1209b	22173	—	XXX
<i>Aulaxina</i> aff. <i>minuta</i> 2	Brazil	Xavier-Leite	1572c	23079	—	XXX
<i>Aulaxina</i> aff. <i>opegraphina</i>	Brazil	Xavier-Leite	1966c	22197	—	XXX
<i>Aulaxina</i> aff. <i>quadrangula</i>	Brazil	Cáceres & Lücking	172	22843	XXX	XXX
<i>Aulaxina</i> aff. <i>quadrangula</i>	Costa Rica	Lücking	sn	22837	XXX	XXX

<i>Aulaxina intermedia</i>	Brazil	Xavier-Leite <i>et al.</i>	1402a	22175	XXX	XXX
<i>Aulaxina minuta</i>	Brazil	Xavier-Leite	1529a	22186	XXX	XXX
<i>Aulaxina minuta</i>	Brazil	Xavier-Leite	1529b	22187	—	XXX
<i>Aulaxina minuta</i>	Brazil	Xavier-Leite	1530b	23033	—	XXX
<i>Aulaxina opegraphina</i>	Brazil	Cáceres & Aptroot	28644	23130	—	XXX
<i>Aulaxina opegraphina</i>	Brazil	Cáceres & Aptroot	28652	23131	XXX	XXX
<i>Aulaxina quadrangula</i>	Brazil	Cáceres & Aptroot	28633	23123	XXX	XXX
<i>Aulaxina quadrangula</i>	Brazil	Cáceres & Aptroot	28638	23124	XXX	XXX
<i>Aulaxina quadrangula</i>	Brazil	Cáceres & Aptroot	28639	23120	XXX	XXX
<i>Aulaxina quadrangula</i>	Brazil	Cáceres & Aptroot	28648	23122	XXX	XXX
<i>Aulaxina quadrangula</i>	Brazil	Cáceres & Aptroot	28650	23121	XXX	XXX
<i>Aulaxina quadrangula</i>	Brazil	Cáceres & Aptroot	28651	23133	XXX	XXX
<i>Aulaxina quadrangula</i>	Brazil	Cáceres & Aptroot	28653	23132	XXX	XXX
<i>Aulaxina quadrangula</i>	Brazil	Cáceres & Aptroot	28671	23125	XXX	XXX
<i>Aulaxina quadrangula</i>	Brazil	Cáceres & Aptroot	28683	23134	XXX	XXX
<i>Aulaxina quadrangula</i>	Brazil	Cáceres & Aptroot	28692	23128	XXX	XXX
<i>Aulaxina quadrangula</i>	Brazil	Cáceres & Aptroot	28664a	23126	XXX	XXX
<i>Aulaxina quadrangula</i>	Brazil	Xavier-Leite	1661	22185	XXX	XXX
<i>Aulaxina quadrangula</i>	Brazil	Xavier-Leite	2452	22114	XXX	XXX
<i>Aulaxina quadrangula</i>	Brazil	Xavier-Leite	2018a	23093	XXX	XXX
<i>Aulaxina quadrangula</i>	Costa Rica				AY341364	AY341350
<i>Aulaxina sp.</i>	Brazil	Xavier-Leite <i>et al.</i>	1139	22162	XXX	XXX
<i>Aulaxina submuralis</i>	Brazil	Xavier-Leite <i>et al.</i>	1148	22163	XXX	XXX
<i>Aulaxina submuralis</i>	Brazil	Xavier-Leite <i>et al.</i>	1303	22188	—	XXX
<i>Bullatina aspidota</i>	Costa Rica	Lücking	10b	22897	—	XXX
<i>Calenia aff. monospora</i>	Costa Rica				KF833339	KF833325
<i>Calenia aff. monospora</i>	Cuba	Lücking <i>et al.</i>	41877b	22929	XXX	XXX
<i>Calenia aff. monospora</i>	Cuba	Lücking <i>et al.</i>	41885c	22934	XXX	XXX
<i>Calenia aff. monospora</i>	Guatemala	Lücking <i>et al.</i>	4531	22815	XXX	—
<i>Calenia bullatinoides</i>	Brazil	Xavier-Leite	2484	23113	—	XXX
<i>Calenia depressa</i>	Costa Rica	Lücking	31	22901	XXX	XXX
<i>Calenia graphidea</i>	Brazil	Xavier-Leite	1958	22070	—	XXX
<i>Calenia graphidea</i>	Brazil	Xavier-Leite	1988	22027	—	XXX
<i>Calenia graphidea</i>	Brazil	Xavier-Leite	2150	22096	—	XXX
<i>Calenia graphidea</i>	Brazil	Xavier-Leite	2348	22189	—	XXX
<i>Calenia graphidea</i>	Brazil	Xavier-Leite	2443	22061	—	XXX
<i>Calenia lobulata</i>	Costa Rica	Lücking	sn	22838	XXX	XXX
<i>Calenia lueckingii</i>	Costa Rica	Lücking	s.n	22839	—	XXX
<i>Calenia lueckingii</i>	Mexico	Herrera <i>et al.</i>	M01	22921	—	XXX
<i>Calenia monospora</i>	Costa Rica				AY341365	AY341351

<i>Calenia phyllogena</i>	Costa Rica				AY341366	AY341352
<i>Calenia phyllogena</i>	Mexico	Herrera <i>et al.</i>	M11	22925	—	XXX
<i>Calenia solorinoides</i>	Costa Rica				KF833337	KF833327
<i>Calenia sp.</i>	Brazil	Xavier-Leite & Cáceres	1756	22044	XXX	XXX
<i>Calenia submuralis</i>	Brazil	Xavier-Leite & Cáceres	1796	22112	XXX	—
<i>Calenia triseptata</i>	Brazil	Cáceres & Aptroot	28640	23135	XXX	XXX
<i>Calenia triseptata</i>	Brazil	Cáceres & Aptroot	28649	23136	—	XXX
<i>Calenia triseptata</i>	Brazil	Cáceres & Aptroot	28655	23137	—	XXX
<i>Calenia triseptata</i>	Brazil	Cáceres & Aptroot	28665b	23148	—	XXX
<i>Calenia triseptata</i>	Brazil	Cáceres & Aptroot	28672b	23146	—	XXX
<i>Caleniopsis laevigata</i>	Brazil	Cáceres & Aptroot	28647	23139	—	XXX
<i>Caleniopsis laevigata</i>	Brazil	Cáceres & Aptroot	28656	23138	—	XXX
<i>Caleniopsis laevigata</i>	Brazil	Cáceres & Aptroot	28667	23142	—	XXX
<i>Caleniopsis laevigata</i>	Brazil	Cáceres & Aptroot	28690	23141	—	XXX
<i>Echinoplaca aff. epiphylla</i> 1	Brazil	Cáceres & Lücking	169	22870	XXX	—
<i>Echinoplaca aff. epiphylla</i> 1	Brazil	Xavier-Leite	1442	22118A	XXX	—
<i>Echinoplaca aff. epiphylla</i> 1	Brazil	Xavier-Leite	1840	23003	XXX	XXX
<i>Echinoplaca aff. epiphylla</i> 1	Brazil	Xavier-Leite	1933	23004	XXX	XXX
<i>Echinoplaca aff. epiphylla</i> 2	unknown				AY648891	—
<i>Echinoplaca aff. lucernifera</i>	Brazil	Xavier-Leite	1927	22084	—	XXX
<i>Echinoplaca aff. lucernifera</i>	Brazil	Xavier-Leite	2541	22067	—	XXX
<i>Echinoplaca aff. marginata</i>	Brazil	Cáceres & Lücking	139	22869	—	XXX
<i>Echinoplaca aff. marginata</i>	Brazil	Xavier-Leite <i>et al.</i>	1242	23013	—	XXX
<i>Echinoplaca aff. marginata</i>	Brazil	Xavier-Leite <i>et al.</i>	1370b	22170	—	XXX
<i>Echinoplaca aff. marginata</i>	Brazil	Xavier-Leite <i>et al.</i>	1397b	22168	—	XXX
<i>Echinoplaca aff. verrucifera</i>	Brazil	Xavier-Leite <i>et al.</i>	2610	22064	—	XXX
<i>Echinoplaca calcarea</i>	Brazil	Xavier-Leite <i>et al.</i>	1262a	22198	XXX	XXX
<i>Echinoplaca calcarea</i>	Brazil	Xavier-Leite <i>et al.</i>	1262b	22199	XXX	XXX
<i>Echinoplaca calcarea</i>	Brazil	Xavier-Leite <i>et al.</i>	1262c	22200	XXX	XXX
<i>Echinoplaca campanulata</i>	Brazil	Cáceres & Lücking	167	22863	XXX	XXX
<i>Echinoplaca campanulata</i>	Brazil	Cáceres & Lücking	168	22846	XXX	XXX
<i>Echinoplaca campanulata</i>	Brazil	Cáceres & Lücking	170b	22854	XXX	XXX
<i>Echinoplaca diffluens</i>	Brazil	Xavier-Leite	1901	23001	—	XXX
<i>Echinoplaca diffluens</i>	Brazil	Xavier-Leite	2001	22011	—	XXX
<i>Echinoplaca diffluens</i>	Mexico				AY341367	AY341353
<i>Echinoplaca epiphylla</i>	Brazil	Cáceres & Lücking	166	22855	XXX	XXX
<i>Echinoplaca epiphylla</i>	Brazil	Cáceres & Lücking	165a	22851	XXX	XXX
<i>Echinoplaca epiphylla</i>	Brazil	Cáceres & Lücking	165b	22852	XXX	XXX
<i>Echinoplaca epiphylla</i>	Brazil	Xavier-Leite	1588	23002	—	XXX
<i>Echinoplaca epiphylla</i>	Brazil	Xavier-Leite	1992	22080	XXX	XXX

<i>Echinoplaca epiphylla</i>	Brazil	Xavier-Leite	2143	22038	XXX	XXX
<i>Echinoplaca epiphylla</i>	Brazil	Xavier-Leite	2583	22092	XXX	XXX
<i>Echinoplaca epiphylla</i>	Brazil	Xavier-Leite	2018b	23094	XXX	XXX
<i>Echinoplaca epiphylla</i>	Brazil	Xavier-Leite & Cáceres	1736	22047	XXX	XXX
<i>Echinoplaca epiphylla</i>	Brazil	Xavier-Leite & Cáceres	1742	22103	XXX	—
<i>Echinoplaca epiphylla</i>	Mexico				AY341368	AY341354
<i>Echinoplaca intercedens</i>	Brazil	Xavier-Leite	2082	23006	—	XXX
<i>Echinoplaca leucotrichoides</i>	Brazil	Cáceres & Lücking	145	22845	—	XXX
<i>Echinoplaca leucotrichoides</i>	Brazil	Cáceres & Lücking	146	22886	—	XXX
<i>Echinoplaca leucotrichoides</i>	Brazil	Xavier-Leite	1523	23009	—	XXX
<i>Echinoplaca leucotrichoides</i>	Brazil	Xavier-Leite	1574	23007	—	XXX
<i>Echinoplaca leucotrichoides</i>	Brazil	Xavier-Leite	1989	22030	XXX	XXX
<i>Echinoplaca leucotrichoides</i>	Brazil	Xavier-Leite	2001	22013	—	XXX
<i>Echinoplaca leucotrichoides</i>	Brazil	Xavier-Leite	1490a	23010	—	XXX
<i>Echinoplaca leucotrichoides</i>	Brazil	Xavier-Leite & Cáceres	1734	22046	XXX	XXX
<i>Echinoplaca leucotrichoides</i>	Brazil	Xavier-Leite & Cáceres	1760	22040	—	XXX
<i>Echinoplaca leucotrichoides</i>	Brazil	Xavier-Leite <i>et al.</i>	1027	23008	XXX	XXX
<i>Echinoplaca leucotrichoides</i>	Brazil	Xavier-Leite <i>et al.</i>	2739	22154	—	XXX
<i>Echinoplaca leucotrichoides</i>	Costa Rica				AY341369	AY341355
<i>Echinoplaca lucernifera</i>	Costa Rica	Lücking	59c	22910	—	XXX
<i>Echinoplaca lucernifera</i>	Costa Rica				AY341370	AY341356
<i>Echinoplaca marginata</i>	Brazil	Cáceres & Lücking	140	22884	—	XXX
<i>Echinoplaca marginata</i>	Brazil	Xavier-Leite	1459	23014	—	XXX
<i>Echinoplaca marginata</i>	Brazil	Xavier-Leite	1466	23015	—	XXX
<i>Echinoplaca marginata</i>	Brazil	Xavier-Leite	1539	23012	—	XXX
<i>Echinoplaca marginata</i>	Brazil	Xavier-Leite	1467b	22184	—	XXX
<i>Echinoplaca marginata</i>	Brazil	Xavier-Leite	1483a	23114	—	XXX
<i>Echinoplaca marginata</i>	Brazil	Xavier-Leite	1527b	23076	—	XXX
<i>Echinoplaca marginata</i>	Brazil	Xavier-Leite	1572b	23078	—	XXX
<i>Echinoplaca neotropica</i>	Brazil	Cáceres & Aptroot	28641	23144	XXX	—
<i>Echinoplaca neotropica</i>	Brazil	Cáceres & Aptroot	28670	23143	—	XXX
<i>Echinoplaca neotropica</i>	Brazil	Xavier-Leite	1907	23016	—	XXX
<i>Echinoplaca neotropica</i>	Brazil	Xavier-Leite	1927	22085	XXX	XXX
<i>Echinoplaca neotropica</i>	Brazil	Xavier-Leite	2041a	23017	—	XXX
<i>Echinoplaca pellicula</i>	Brazil	Cáceres & Lücking	137	22871	—	XXX
<i>Echinoplaca pellicula</i>	Brazil	Xavier-Leite	1501	23021	—	XXX
<i>Echinoplaca pellicula</i>	Brazil	Xavier-Leite	1502	23019	—	XXX
<i>Echinoplaca pellicula</i>	Brazil	Xavier-Leite	1560	23020	—	XXX
<i>Echinoplaca pellicula</i>	Guatemala	Lücking	4476	22821	—	XXX
<i>Echinoplaca sp.</i>	Brazil	Xavier-Leite	1915	22093	—	XXX

<i>Echinoplaca</i> sp.	Brazil	Xavier-Leite	1928	22083	—	XXX
<i>Echinoplaca</i> sp.	Brazil	Xavier-Leite	1983	22019	—	XXX
<i>Echinoplaca</i> sp.	Brazil	Xavier-Leite	2582	22091	—	XXX
<i>Echinoplaca</i> sp.	Cuba	Lücking <i>et al.</i>	42473	22938	—	XXX
<i>Echinoplaca</i> sp.	Nicaragua				KF833340	KF833328
<i>Echinoplaca</i> sp. nov.	Brazil	Xavier-Leite	1986	22024	—	XXX
<i>Echinoplaca</i> sp. nov.	Brazil	Xavier-Leite & Cáceres	1718	23023	XXX	XXX
<i>Echinoplaca</i> sp. nov.	Guatemala	Lücking	4473	22825	—	XXX
<i>Echinoplaca</i> sp. nov.	Panama	Lücking	519	22893	—	XXX
<i>Echinoplaca tetrapla</i>	Brazil	Xavier-Leite <i>et al.</i>	1364	23100	—	XXX
<i>Echinoplaca tetrapla</i>	Brazil	Xavier-Leite <i>et al.</i>	1422	22177	—	XXX
<i>Echinoplaca tetrapla</i>	Brazil	Xavier-Leite <i>et al.</i>	1397a	22167	—	XXX
<i>Echinoplaca urceolata</i>	Brazil	Cáceres & Lücking	171	22873	XXX	XXX
<i>Echinoplaca verrucifera</i>	Brazil	Xavier-Leite	1955	22001	XXX	XXX
<i>Echinoplaca verrucifera</i>	Brazil	Xavier-Leite	1988	22025	XXX	—
<i>Echinoplaca verrucifera</i>	Brazil	Xavier-Leite	2541	22068	XXX	XXX
<i>Echinoplaca verrucifera</i>	Brazil	Xavier-Leite	2545	22069	XXX	XXX
<i>Gomphillus calycioides</i>	Scotland				KF833341	KF833329
<i>Gomphillus ophiosporus</i>	Costa Rica				AY341371	AY341357
<i>Gyalectidium</i> aff. <i>filicinum</i>	Brazil	Xavier-Leite	1951	22010	XXX	XXX
<i>Gyalectidium</i> aff. <i>filicinum</i>	Brazil	Xavier-Leite	1978	22073	—	XXX
<i>Gyalectidium</i> aff. <i>filicinum</i>	Brazil	Xavier-Leite	2002	22017	—	XXX
<i>Gyalectidium</i> aff. <i>imperfectum</i>	Brazil	Xavier-Leite	1973	22005	XXX	XXX
<i>Gyalectidium</i> aff. <i>imperfectum</i>	Brazil	Xavier-Leite	1978	22075	XXX	XXX
<i>Gyalectidium</i> aff. <i>imperfectum</i>	Brazil	Xavier-Leite	1997	22034	XXX	XXX
<i>Gyalectidium</i> aff. <i>imperfectum</i>	Brazil	Xavier-Leite	2004	22014	XXX	XXX
<i>Gyalectidium</i> aff. <i>imperfectum</i>	Costa Rica	Lücking	55	22908	XXX	XXX
<i>Gyalectidium</i> aff. <i>imperfectum</i>	Guatemala	Lücking	4353	22807	XXX	XXX
<i>Gyalectidium</i> aff. <i>imperfectum</i>	Guatemala	Lücking	4474	22822	XXX	XXX
<i>Gyalectidium</i> aff. <i>imperfectum</i>	Guatemala	Lücking	4479	22836	—	XXX
<i>Gyalectidium areolatum</i>	Brazil	Xavier-Leite	2061	23103	—	XXX
<i>Gyalectidium areolatum</i>	Brazil	Xavier-Leite	2085b	23105	—	XXX
<i>Gyalectidium areolatum</i>	Brazil	Xavier-Leite	2096a	23101	—	XXX
<i>Gyalectidium catenulatum</i>	Costa Rica				KF833335	KF833323
<i>Gyalectidium caucasicum</i>	Brazil	Xavier-Leite	2085c	23106	—	XXX
<i>Gyalectidium denticulatum</i>	Brazil	Xavier-Leite	2096b	23102	—	XXX
<i>Gyalectidium denticulatum</i>	Brazil	Xavier-Leite <i>et al.</i>	1245	23024	XXX	XXX
<i>Gyalectidium filicinum</i>	Brazil	Cáceres & Lücking	142	22857	XXX	XXX
<i>Gyalectidium filicinum</i>	Brazil	Xavier-Leite	1263	22171	XXX	XXX
<i>Gyalectidium filicinum</i>	Brazil	Xavier-Leite	1520	23031	—	XXX

<i>Gyalectidium filicinum</i>	Brazil	Xavier-Leite	1801	23029	—	XXX
<i>Gyalectidium filicinum</i>	Brazil	Xavier-Leite	1935	23027	—	XXX
<i>Gyalectidium filicinum</i>	Brazil	Xavier-Leite	1970	22007	XXX	XXX
<i>Gyalectidium filicinum</i>	Brazil	Xavier-Leite	2015	23028	—	XXX
<i>Gyalectidium filicinum</i>	Brazil	Xavier-Leite	2148	22095	XXX	XXX
<i>Gyalectidium filicinum</i>	Brazil	Xavier-Leite	2481	23025	—	XXX
<i>Gyalectidium filicinum</i>	Brazil	Xavier-Leite	1490b	23011	XXX	XXX
<i>Gyalectidium filicinum</i>	Brazil	Xavier-Leite	1530a	23032	—	XXX
<i>Gyalectidium filicinum</i>	Brazil	Xavier-Leite	1571b	23074	XXX	XXX
<i>Gyalectidium filicinum</i>	Brazil	Xavier-Leite & Cáceres	1756	22045	—	XXX
<i>Gyalectidium filicinum</i>	Brazil	Xavier-Leite <i>et al.</i>	1042	23034	—	XXX
<i>Gyalectidium imperfectum</i>	Brazil	Xavier-Leite	1801	23030	—	XXX
<i>Gyalectidium imperfectum</i>	Brazil	Xavier-Leite	2041b	23018	XXX	XXX
<i>Gyalectidium imperfectum</i>	Brazil	Xavier-Leite <i>et al.</i>	1074	23040	—	XXX
<i>Gyalectidium imperfectum</i>	Brazil	Xavier-Leite <i>et al.</i>	1368	23041	—	XXX
<i>Gyalectidium imperfectum</i>	Costa Rica				AY341372	AY341358
<i>Gyalectidium imperfectum</i>	Cuba	Lücking <i>et al.</i>	41737	22926	XXX	XXX
<i>Gyalectidium sp.</i>	Brazil	Cáceres & Lücking	143	22876	XXX	XXX
<i>Gyalectidium sp.</i>	Brazil	Xavier-Leite	1986	22023	XXX	XXX
<i>Gyalidea fritzei</i>	Sweden				HM244744	HM244767
<i>Gyalidea hyalinescens</i>	unknown				DQ972996	DQ973046
<i>Gyalideopsis aff. vulgaris</i>	Brazil	Xavier-Leite <i>et al.</i>	1188	23051	—	XXX
<i>Gyalideopsis aff. vulgaris</i>	Brazil	Xavier-Leite <i>et al.</i>	1198	23047	—	XXX
<i>Gyalideopsis applanata</i>	Brazil	Xavier-Leite <i>et al.</i>	1321	22165	—	XXX
<i>Gyalideopsis epithallina</i>	Brazil	Xavier-Leite <i>et al.</i>	1030	23107	—	XXX
<i>Gyalideopsis sp.</i>	Costa Rica				AY341373	AY341359
<i>Gyalideopsis sp. nov.</i>	Brazil	Xavier-Leite	1483b	23115	—	XXX
<i>Gyalideopsis sp.-nova</i>	Brazil	Xavier-Leite	1470	23109	—	XXX
<i>Gyalideopsis vulgaris</i>	Brazil	Xavier-Leite	1476	23108	—	XXX
<i>Gyalideopsis vulgaris</i>	Brazil	Xavier-Leite <i>et al.</i>	2229	22145	—	XXX
<i>Gyalideopsis vulgaris</i>	unknown				AY584618	—
<i>Gyalideopsis vulgaris f. albomarginata</i>	Brazil	Xavier-Leite <i>et al.</i>	1196	23046	—	XXX
<i>Gyalideopsis vulgaris f. albomarginata</i>	Brazil	Xavier-Leite <i>et al.</i>	1109a	23052	—	XXX
<i>Jamesiella anastomosans</i>	Netherlands	Aptroot	75525	MON5443m		—
<i>Linhartia patellarioides</i>	Brazil	Xavier-Leite <i>et al.</i>	1096	23112	—	XXX
<i>Psorotheciopsis cf. premneella</i>	Cuba	Lücking <i>et al.</i>	41885b	22933	—	XXX
<i>Rolueckia aff. conspersa</i>	Brazil	Xavier-Leite <i>et al.</i>	2950	22150	—	XXX
<i>Rolueckia aggregata</i>	Brazil	Cáceres & Aptroot	28681	23151	—	XXX
<i>Rolueckia aggregata</i>	Brazil	Cáceres & Aptroot	28665a	23147	—	XXX
<i>Rolueckia aggregata</i>	Brazil	Cáceres & Aptroot	28672a	23145	—	XXX

<i>Rolueckia conspersa</i>	Brazil	Xavier-Leite <i>et al.</i>	2803	22156	—	XXX
<i>Rubrotricha subhelminthospora</i>	Brazil	Xavier-Leite <i>et al.</i>	2414	22132	XXX	—
<i>Rubrotricha subhelminthospora</i>	Brazil	Xavier-Leite <i>et al.</i>	2420	22127	XXX	—
<i>Rubrotricha subhelminthospora</i>	Brazil	Xavier-Leite <i>et al.</i>	2629	22149	XXX	XXX
<i>Rubrotricha subhelminthospora</i>	Brazil	Xavier-Leite <i>et al.</i>	2790	22098	XXX	XXX
<i>Tricharia aff. carnea</i>	Brazil	Xavier-Leite & Cáceres	1759	22042	XXX	—
<i>Tricharia aff. carnea</i>	Guatemala	Lücking	4388	22833	XXX	XXX
<i>Tricharia aff. farinosa</i>	Guatemala	Lücking	4344	22809	—	XXX
<i>Tricharia aff. farinosa</i>	Guatemala	Lücking	4345	22801	XXX	XXX
<i>Tricharia aff. hyalina</i>	Brazil	Xavier-Leite	1054	22089	—	XXX
<i>Tricharia aff. longispora</i>	Costa Rica	Lücking	70	22913	XXX	—
<i>Tricharia aff. vainioi</i>	Brazil	Xavier-Leite	1981	22078	XXX	XXX
<i>Tricharia amazonum</i>	Brazil	Xavier-Leite	1498	23058	—	XXX
<i>Tricharia amazonum</i>	Brazil	Xavier-Leite	1517	23059	—	XXX
<i>Tricharia amazonum</i>	Brazil	Xavier-Leite	1576	23057	—	XXX
<i>Tricharia amazonum</i>	Brazil	Xavier-Leite	1991	22032	—	XXX
<i>Tricharia amazonum</i>	Brazil	Xavier-Leite	2010	22087	—	XXX
<i>Tricharia amazonum</i>	Brazil	Xavier-Leite	1568a	23060	—	XXX
<i>Tricharia amazonum</i>	Brazil	Xavier-Leite & Cáceres	1701	22050	—	XXX
<i>Tricharia amazonum</i>	Guatemala	Lücking	4480	22834	—	XXX
<i>Tricharia carnea</i>	Costa Rica	Lücking	91	22919	XXX	—
<i>Tricharia farinosa</i>	Brazil	Xavier-Leite	1953	22076	—	XXX
<i>Tricharia farinosa</i>	Brazil	Xavier-Leite	1955	22002	—	XXX
<i>Tricharia farinosa</i>	Brazil	Xavier-Leite	1970	22006	—	XXX
<i>Tricharia farinosa</i>	Brazil	Xavier-Leite	1978	22074	—	XXX
<i>Tricharia farinosa</i>	Brazil	Xavier-Leite	2002	22018	—	XXX
<i>Tricharia farinosa</i>	Brazil	Xavier-Leite	2029	23062	—	XXX
<i>Tricharia farinosa</i>	Brazil	Xavier-Leite <i>et al.</i>	1218	23063	—	XXX
<i>Tricharia farinosa</i>	Brazil	Xavier-Leite <i>et al.</i>	1360	23065	—	XXX
<i>Tricharia farinosa</i>	Brazil	Xavier-Leite <i>et al.</i>	1363	23064	—	XXX
<i>Tricharia hyalina</i>	Brazil	Cáceres & Aptroot	28636	23153	—	XXX
<i>Tricharia hyalina</i>	Brazil	Cáceres & Aptroot	28642a	23154	—	XXX
<i>Tricharia hyalina</i>	Brazil	Cáceres & Aptroot	28642b	23155	—	XXX
<i>Tricharia lancicarpa</i>	Brazil	Xavier-Leite	1564	23067	XXX	XXX
<i>Tricharia lancicarpa</i>	Brazil	Xavier-Leite <i>et al.</i>	1316	23066	XXX	XXX
<i>Tricharia lancicarpa</i>	Brazil	Xavier-Leite <i>et al.</i>	1318	22164	XXX	XXX
<i>Tricharia lancicarpa</i>	Brazil	Xavier-Leite <i>et al.</i>	1302b	23099	—	XXX
<i>Tricharia longispora</i>	Brazil	Cáceres & Aptroot	28645	23156	XXX	XXX
<i>Tricharia longispora</i>	Brazil	Cáceres & Lücking	138	22872	—	XXX
<i>Tricharia longispora</i>	Brazil	Xavier-Leite <i>et al.</i>	2625	22148	XXX	XXX

<i>Tricharia longispora</i>	Brazil	Xavier-Leite <i>et al.</i>	2971	22142	—	XXX
<i>Tricharia longispora</i>	Brazil	Xavier-Leite <i>et al.</i>	3010	22160	XXX	XXX
<i>Tricharia longispora</i>	Costa Rica				AY341374	AY341360
<i>Tricharia longispora</i>	Costa Rica				KF833338	KF833326
<i>Tricharia longispora</i>	Mexico	Herrera <i>et al.</i>	M04	22922	—	XXX
<i>Tricharia longispora</i>	Mexico	Herrera <i>et al.</i>	M10	22924	—	XXX
<i>Tricharia paraguayensis</i>	Brazil	Xavier-Leite	1589	23072	XXX	XXX
<i>Tricharia paraguayensis</i>	Brazil	Xavier-Leite	2581	23056	XXX	XXX
<i>Tricharia paraguayensis</i>	Brazil	Xavier-Leite & Cáceres	1768	22101	XXX	—
<i>Tricharia similis</i>	Brazil	Xavier-Leite <i>et al.</i>	2395	22126	XXX	—
<i>Tricharia similis</i>	Brazil	Xavier-Leite <i>et al.</i>	2754	22147	XXX	—
<i>Tricharia sp.</i>	Brazil	Xavier-Leite	1950	22009	XXX	XXX
<i>Tricharia sp.</i>	Brazil	Xavier-Leite	1990	22031	XXX	—
<i>Tricharia sp.</i>	Brazil	Xavier-Leite & Cáceres	1738	22049	XXX	—
<i>Tricharia sp.</i>	Guatemala	Lücking	4476	22831	XXX	—
<i>Tricharia sp. nov.</i>	Brazil	Xavier-Leite	2143	22037	—	XXX
<i>Tricharia sp. nov.</i>	Brazil	Xavier-Leite	2344	22059	XXX	XXX
<i>Tricharia sp. nov.</i>	Brazil	Xavier-Leite & Cáceres	2494	22052	XXX	XXX
<i>Tricharia sp. nov.</i>	Brazil	Xavier-Leite <i>et al.</i>	2409	22107	XXX	—
<i>Tricharia urceolata</i>	Brazil	Cáceres & Lücking	176b	22848	—	XXX
<i>Tricharia urceolata</i>	Brazil	Xavier-Leite	1473a	23068	—	XXX
<i>Tricharia urceolata</i>	Brazil	Xavier-Leite	1473b	23069	—	XXX
<i>Tricharia urceolata</i>	Brazil	Xavier-Leite	1473c	23070	—	XXX
<i>Tricharia urceolata</i>	Brazil	Xavier-Leite & Cáceres	1678	22051	—	XXX
<i>Tricharia urceolata</i>	Cuba	Lücking <i>et al.</i>	41875	22927	XXX	XXX
<i>Tricharia urceolata</i>	Guatemala	Lücking	4482	22820	—	XXX
<i>Tricharia vainioi</i>	Brazil	Cáceres & Lücking	153	22877	XXX	—
<i>Tricharia vainioi</i>	Brazil	Cáceres & Aptroot	28643	23157	XXX	XXX
<i>Tricharia vainioi</i>	Brazil	Xavier-Leite	1519	23080	—	XXX
<i>Tricharia vainioi</i>	Brazil	Xavier-Leite	1556	23111	XXX	—
<i>Tricharia vainioi</i>	Brazil	Xavier-Leite	1956	22004	—	XXX
<i>Tricharia vainioi</i>	Brazil	Xavier-Leite	1986	22021	XXX	—
<i>Tricharia vainioi</i>	Brazil	Xavier-Leite	2004	22015	XXX	—
<i>Tricharia vainioi</i>	Brazil	Xavier-Leite	1527a	23075	XXX	—
<i>Tricharia vainioi</i>	Brazil	Xavier-Leite	1571a	23073	XXX	—
<i>Tricharia vainioi</i>	Brazil	Xavier-Leite	1572a	23077	XXX	XXX
<i>Tricharia vainioi</i>	Brazil	Xavier-Leite <i>et al.</i>	1402b	22176	XXX	XXX
<i>Tricharia vainioi</i>	Costa Rica				KF833336	KF833324
<i>Tricharia vainioi</i>	Panama	Lücking	520	22890	XXX	—

The phylogenetic analysis based on the two data set resulted in nearly 40 clades corresponding mostly to previously recognized genera, but also to some new lineages, with distinct supports (Fig. 1–4). The first diverging lineage was the recently established genus *Rolueckia* (Pamong *et al.* 2008), this topology was supported (Fig. 2). Next, there is a supported clade including the two genera *Psorotheciopsis* and *Gyalidea*, but the position of this clade, which corresponds to the previously separated families Asterothyriaceae p.p. and Solorinellaceae, again was not supported. A further, supported clade includes four lineages, the *Calenia triseptata* aggregate, differing from *Calenia* s.str. in the small, 3-septate ascospores and absence of hyphophores (new genus *Caleniella*), the *Aulaxina minuta* aggregate, differing from *Aulaxina* in the dark brown prothallus (new genus *Aulaxinella*), the genus *Caleniopsis*, and the genus *Aulaxina* s.str. Subsequently, another supported clade includes *Calenia monospora*, a morphologically unique taxon with smooth thallus and short hyphophores (new genus *Monocalenia*) and a supported clade with the genus *Linhartia*, represented by *L. patellarioides*, and the genus *Asterothyrium*, with several species (former family Asterothyriaceae p.p.). However, the genus *Asterothyrium*, excluding *Linhartia* was not supported. The next unsupported clade contains a supported clade with the morphologically aberrant *Calenia solorinoides* plus an unidentified species forming hyphophores only and akin towards *C. monospora* (new genus *Pseudocalenia*), a supported clade corresponding to the *Aderkomyces purulhensis* aggregate, with chroodiscoid apothecia (new genus *Roselviria*), and a supported clade including the genus *Rubrotricha* and the *Tricharia farinosa* aggregate, with strongly pruinose apothecia (new genus *Serusiauxiella*). The genus *Jamesiella* forms an unsupported sister group related to the supported *Aderkomyces albostrigosus* group, with sessile, distinctly marginate apothecia (reinstated genus *Spinomyces*), which is then followed by a large, supported clade corresponding to the genus *Gyalectidium* (Fig. 2).

The next large clade, also supported, corresponds to the *Tricharia vainioi* group, with smooth thallus and short setae (reinstated genus *Microxyphiomyces*; Fig. 3). This clade is followed by an unsupported clade containing the *Calenia lobulata* group, the monospecific genus *Bullatina*, and the *Echinoplaca marginata* aggregate, with plane, yet marginate apothecia (new genus *Aptrootidea*). The next part of the tree contains a paraphyletic assemblage of lineages corresponding mostly to species currently placed in the genera *Calenia* s.lat. and *Echinoplaca* s.lat., including the type species of *Calenia* (*C. depressa*), but also a small clade containing specimens referable to *Gyalideopsis* s.lat. Apparently, these grade species with calenioid and echinoplacoid apothecia form complex, unresolved

relationships; notably, *Echinoplaca* s.str. and several other echinoplacoid taxa are not part of this assemblage. Nested within this grade, but strongly supported on long branches, are the genus *Actinoplaca* and the *Gyalideopsis vulgaris* aggregate, with a unique apothecial anatomy and unique hyphophores (new genus *Vezdamyces*). Another strongly supported clade on a long branch is formed by *Echinoplaca diffluens* clade, but this clade is deeply nested within the *Calenia-Echinoplaca* grade (Fig. 3).

The last part of the tree (Fig. 4) starts with a small, supported clade corresponding to the genus *Aderkomyces* s.str., followed by a large, supported clade containing species of *Tricharia* s.str.. This clade is followed by a small clade containing *Gyalideopsis epithallina* group, lichenicolous species with small apothecia and very small ascospores (new genus *Adelphomyces*) and *Tricharia hyalina* complex (new genus *Batistomyces*), which is morphologically similar to the *T. vainioi* group but has short setae and vertically elongate apothecia.

Following a single species of *Gyalideopsis* s.lat., the next, supported clade contains the genera *Gomphillus* (supported), *Arthotheliopsis*, *Echinoplaca neotropica* aggregate, with furcate hyphophores (supported; new genus *Sipmanidea*), the *Aderkomyces heterellus* group, with orange-yellow apothecia and large hyphophores (supported, reinstated genus *Psathyromyces*), and *Echinoplaca verrucifera* group, with a strongly verrucose thallus, marginally pruinose apothecia, and hyphophores formed on the prothallus (supported; new genus *Verruciplaca*). This clade is followed by the supported *E. leucotrichoides* aggregate, with unique hyphophores and diahyphae (reinstated genus *Sporocybomyces*) and an unsupported terminal clade containing a further species of *Gyalideopsis* s.lat., the *E. lucernifera* aggregate, with unique diahyphae (new genus *Bezerroplaca*), and *Echinoplaca* s.str. (Fig. 4). The singleton *Gyalideopsis applanata* in this part of the tree may stand representative for the bulk of foliicolous taxa currently referred to *Gyalideopsis* s.lat. and likely unrelated to the type species, *G. peruviana* Vězda, but since only one species of this group was included in the analysis, we refrain from recognizing this group as a distinct genus.

For the species-level names for which more than one specimen were available, four distinct phylogenetic topologies were observed: (1) forming a monophyletic clade corresponding to single species; (2) forming a monophyletic clade but with internal structure suggesting a complex of more than one species; (3) forming a paraphyletic grade; and (4) polyphyletic. Most taxa formed monophyletic clades corresponding to single species (listed in topological order): *Rolueckia aggregata*, *Calenia triseptata*, *Caleniopsis laevigata*, *Asterothyrium rotuliforme*, *Aderkomyces purulhensis*, *Rubrotricha subhelminthospora* (Fig.

2), *Tricharia lancicarpa*, *Echinoplaca pellicula*, *Gyalideopsis* sp. nov., *Calenia phyllogena*, *C. lueckingii*, *Echinoplaca tetrapla* (Fig. 3), *Aderkomyces* cf. *planicarpus*, *Aderkomyces* sp. nov., *Tricharia paraguayensis*, *Tricharia* sp. nov., *T. amazonum*, *T. hyalina*, *Echinoplaca neotropica*, *E. calcarea*, *E. leucotrichoides* (Fig. 4). Monophyletic clades with internal structure suggesting more than one species were detected in *Aulaxina minuta*, *Asterothyrium leucophthalmum*, *A. microsporum*, *Tricharia farinosa* (Fig. 2), *T. vainioi*, *Echinoplaca marginata*, *E. diffluens*, *Calenia graphidea*, *Actinoplaca strigulacea*, *Gyalectidium vulgare* (Fig. 3), *Tricharia urceolata*, *T. longispora*, and *Echinoplaca verrucifera* (Fig. 4). One taxon, *Aulaxina quadrangula*, formed a paraphyletic grade (Fig. 2). Apparently of polyphyletic nature are taxa identified as *Aulaxina opegraphina*, *Calenia monospora*, *Gyalectidium areolatum*, *G. denticulatum*, *G. filicinum*, *G. imperfectum* (Fig. 2), *Echinoplaca lucernifera* (Fig. 3, 4), *Tricharia carnea*, *Echinoplaca epiphylla*, and *E. campanulata* (Fig. 4). In the case of *Calenia monospora*, *Echinoplaca lucernifera*, and *Gyalectidium* species, specimens identified with the same names, i.e. sharing a similar morphology, were even placed in distinct clades or genus-level lineages.

Due to lack of support in the backbone, while individual genus-level lineages are without exception internally rather uniform in terms of their phenotype, the evolutionary history of particular thalli, apothecial and hyphophore types cannot be traced with confidence. Thus, taxa forming sterile, black or white setae, do not form monophyletic groups each but the genera representing these morphologies are apparently unrelated and dispersed over the tree, as shown by the distant position of the *Tricharia farinosa* aggregate, the *T. vainioi* group, and the *T. hyalina* aggregate versus *Tricharia* s.str., or the *Aderkomyces albostrigosus* and *A. purulhensis* aggregates versus *Aderkomyces* s.str. (Fig. 1–4). Likewise, lineages with sessile and biatorine to adnate and emarginate, to erumpent and zeorine apothecia are scattered over the tree, and there is little correlation of larger clades or portions of the tree with hyphophore type (Fig. 1–4). An exception is the *Aulaxinella-Caleniopsis-Aulaxina* clade, with a unique type of short hyphophores and unique diahyphae formed on an algal-free prothallus. In contrast, other supported clades include morphologically disparate elements, such as *Rubrotricha* versus *Tricharia farinosa* aggregate, which differ in almost every conceivable character. It is, however, notable that lineages with zeorine apothecia are concentrated among the earlier diverging lineages.

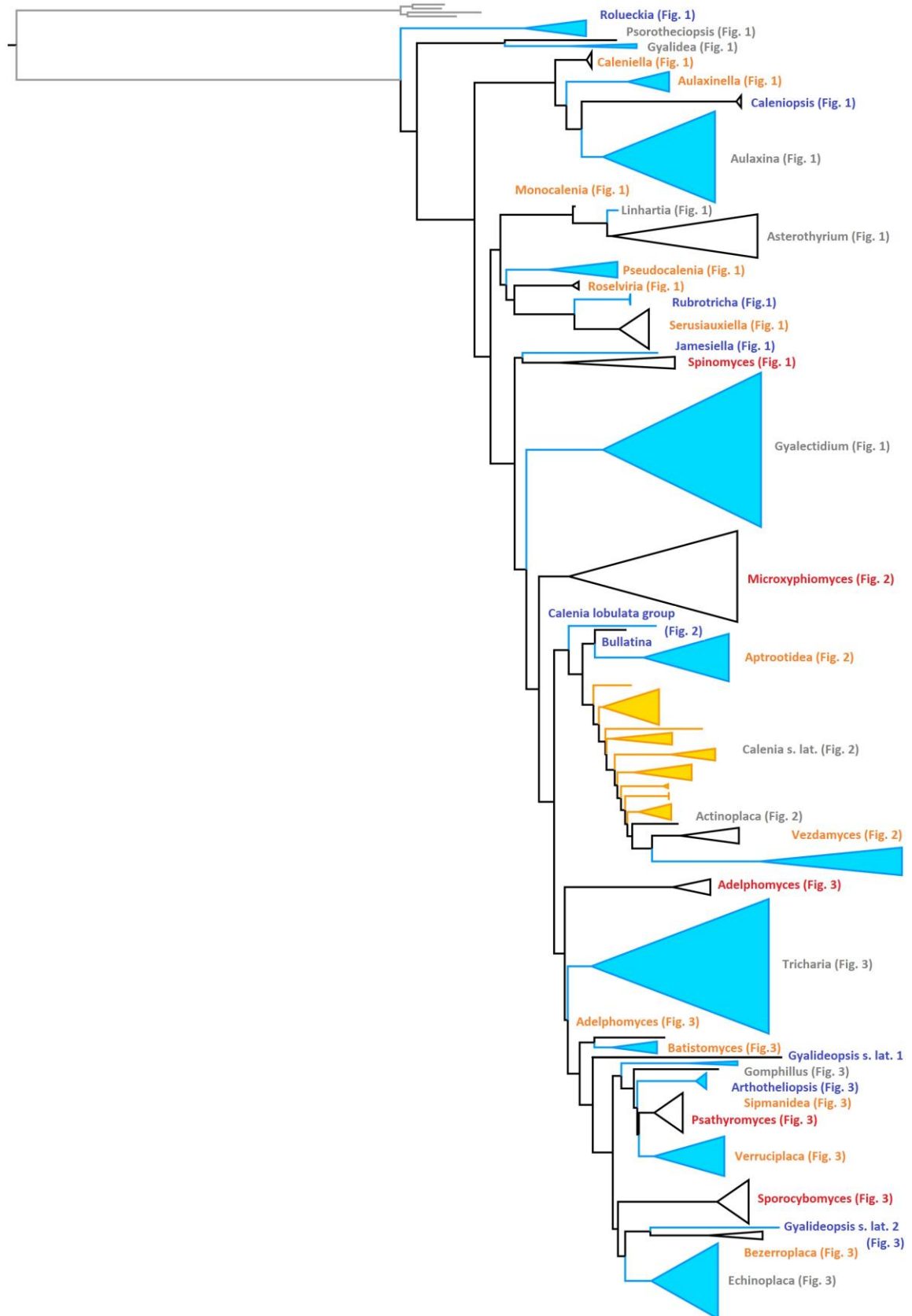


Figure 1: Overall cartoon phylogeny of Gomphillaceae as inferred from a two gene concatenated, maximum-likelihood analysis of mtSSU and nuLSU rDNA data. Details including bootstrap support values are given in the corresponding figures (Fig. 2–4).

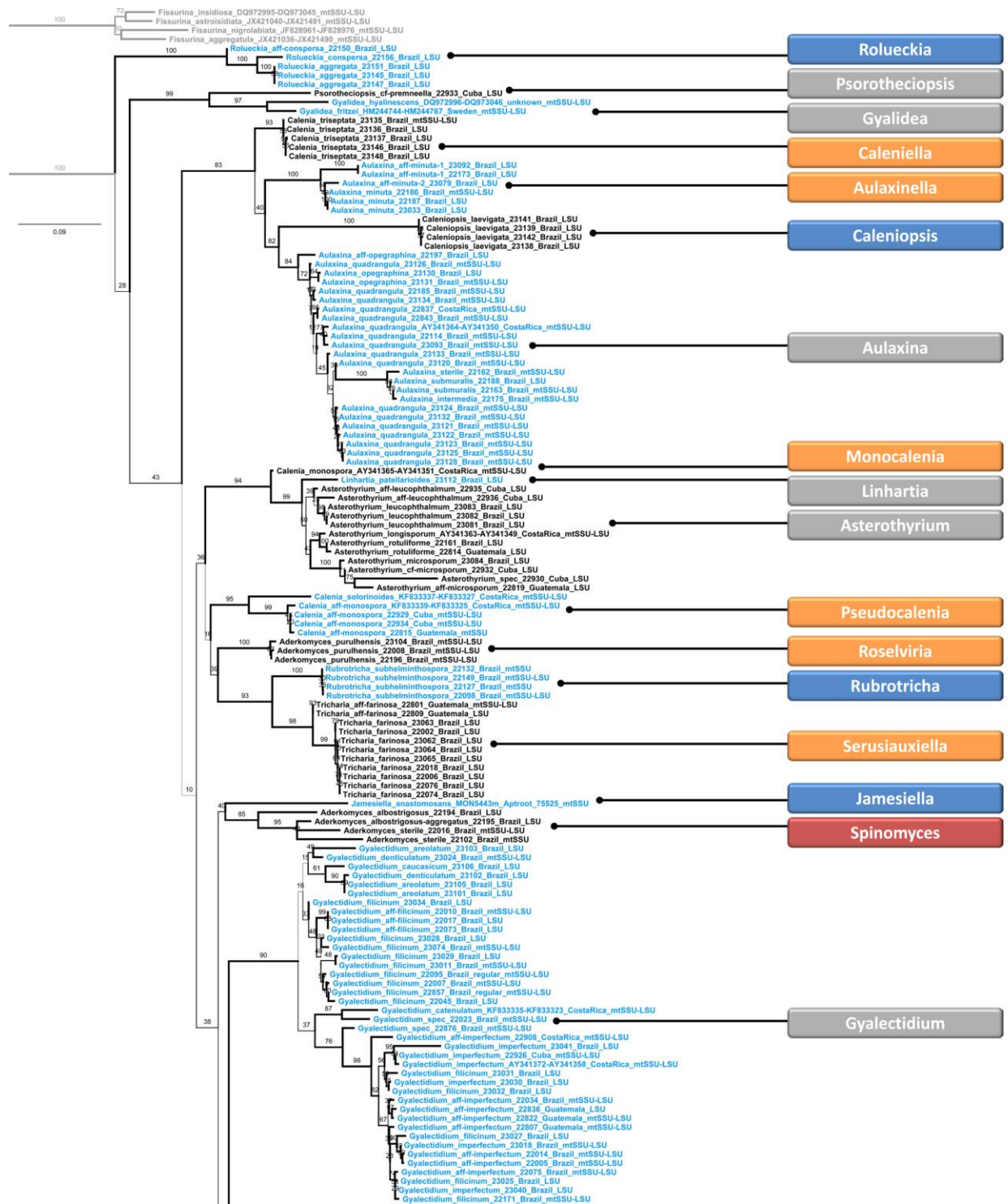


Figure 2: Partial phylogeny of Gomphillaceae (best-scoring maximum likelihood tree) showing details in the basal portion of the tree. Bootstrap values are indicated below the branches. Alternating colors (blue versus black) indicating lineages recognized at genus level, and Labels indicate applicable, available, and newly suggested genus names as follows: grey = long established names; blue = more recently established names; red = names based on Batista and co-workers for hyphophore anamorphs; orange = newly proposed names.

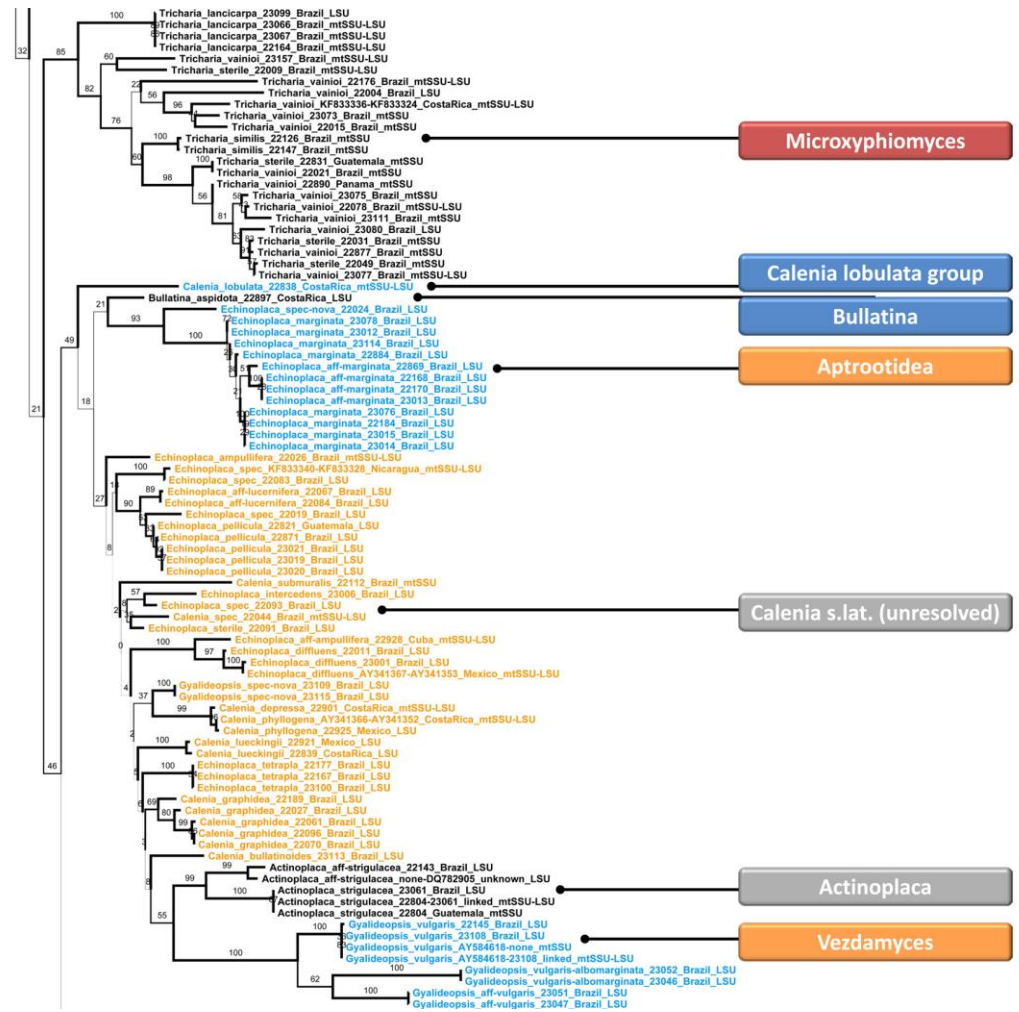


Figure 3: Partial phylogeny of Gomphillaceae (best-scoring maximum likelihood tree) showing details in the mid portion of the tree. Bootstrap values are indicated below the branches. Alternating colors (blue versus black) indicating lineages recognized at genus level, and Labels indicate applicable, available, and newly suggested genus names as follows: grey = long established names; blue = more recently established names; red = names based on Batista and co-workers for hyphophore anamorphs; orange = newly proposed names.

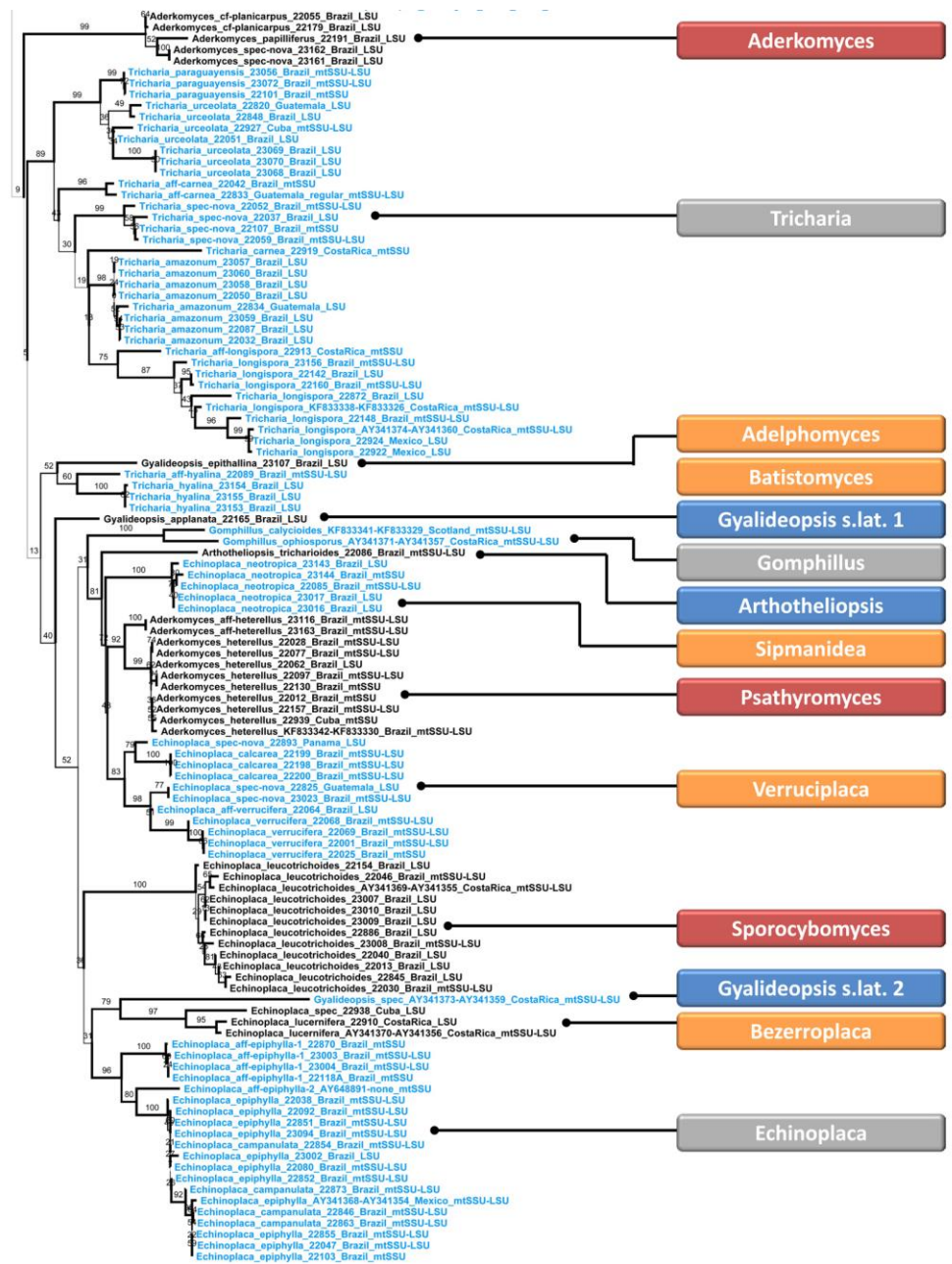


Figure 4: Partial phylogeny of Gomphillaceae (best-scoring maximum likelihood tree) showing details in the apical portion of the tree. Bootstrap values are indicated below the branches. Alternating colors (blue versus black) indicating lineages recognized at genus level, and Labels indicate applicable, available, and newly suggested genus names as follows: grey = long established names; blue = more recently established names; red = names based on Batista and co-workers for hyphophore anamorphs; orange = newly proposed names.

4. DISCUSSION

This study is the first broad approach towards a molecular phylogeny of one of the largest families of lichen fungi. Our results confirm that the genera formerly and variously separated in the families Asterothyriaceae and Solorinellaceae (*Asterothyrium*, *Gyalidea*, *Linhartia*, *Psorotheciopsis*; Vězda 1973; Vězda & Poelt 1987; Lücking 1997, 1999, 2008; Aptroot & Lücking 2002; Henssen & Lücking 2002; Lücking *et al.* 2004, 2005) are not only deeply nested within Gomphillaceae but also do not seem to form monophyletic groups, suggesting that unbranched paraphyses and loss of hyphophores evolved independently within the family. The backbone support for this conclusion is mostly absent, but the inclusion of *Calenia monospora*, with a typical morphology and anatomy of Gomphillaceae, in a supported clade with *Asterothyrium*, supports this assumption. Even if nested within Gomphillaceae, the genera formerly included in Asterothyriaceae according to Lücking (1999) and Henssen & Lücking (2002) were expected to form a monophyletic group, which was not confirmed. The separation of *Psorotheciopsis* from *Asterothyrium* and *Linhartia* was thereby particularly surprising, as all three share a unique thallus anatomy with a cortex composed of regularly radiating cell rows and there are several similarities in ascospore types (Henssen & Lücking 2002).

The lack of backbone support underlines the necessity for additional markers to clarify the deep phylogeny of Gomphillaceae, although it is also possible that this group is based on a rapid radiation and even further markers or a genome skimming approach may not increase backbone resolution and support. As sister to Graphidaceae, for which a Jurassic origin has been reconstructed (Lücking *et al.* 2013), Gomphillaceae also has a deep stem node age but their very long stem branch (Lücking *et al.* 2004; Baloch *et al.* 2010; Rivas Plata 2011) and strongly compressed basal crown support the notion of a rapid diversification that likely initiated in the Late Cretaceous around the K-Pg boundary (Rivas Plata 2011). In contrast to the unresolved backbone, the combination of the two data set mtSSU and nuLSU resolved genus-level lineages quite well in our analysis, with the exception of the paraphyletic assembly containing most species currently assigned to *Calenia* s.lat. and *Echinoplaca* s.lat. We propose in a next step to add at least one protein-coding marker such as *RPB2*, which has being informative in the related Graphidaceae (Lücking *et al.* 2013; Rivas Plata *et al.* 2013), to clarify the complex assemblages in the family.

Our results strongly support the notion that a combination of thallus, apothecial and hyphophore features denote genus-level lineages in the family. This is reflected in the dramatic increase in the number of genera recognized, from seven (Santesson 1952) to 24

(Lücking *et al.* 2017), to now well over 40 based on this analysis. While Santesson (1952) had not yet recognized the hyphophores as an intrinsic structure of the corresponding lichen fungi, and therefore based his concept on thallus and apothecial features, subsequent studies incorporated hyphophore characters into the classification and also reassessed variation in thallus and apothecial features, leading to the recognition of numerous new taxa, such as *Actinoplaca*, *Aderkomyces*, *Aplanocalenia*, *Arthotheliopsis*, *Bullatina*, *Caleniopsis*, *Diploschistella*, *Ferraroa*, *Gyalideopsis*, *Hippocrepidea*, *Jamesiella*, *Lithogyalideopsis*, *Paratracharia*, *Phyllogyalidea*, *Rolueckia*, and *Rubrotricha* (Vězda 1973; Vězda & Poelt 1987; Sérusiaux 1997; Lücking 1997, 2008; Lücking *et al.* 2005; Papong *et al.* 2008). For instance, the genus *Rubrotricha* was established as a new genus separate from *Tricharia* s.lat. and *Aderkomyces* by Lücking *et al.* (2005) due to its reddish brown setae, and this separation was confirmed here.

In previous studies based on phenotype characters, it was already anticipated that larger genera with substantial morphological variation, such as *Aderkomyces*, *Calenia*, *Echinoplaca*, *Gyalideopsis*, and *Tricharia*, were likely not monophyletic (Lücking *et al.* 2005), and so the further increase by an additional 17 genera newly recognized (13 to be described as new, four reinstated) does not come as a surprise; in fact, all but one (*Aulaxinella*) of the newly recognized genera are further segregates of the aforementioned five large genera. A good example is *Tricharia* s.lat., which included various groups distinguished by thallus and apothecial morphology; thus, *Tricharia* s.str. is restricted to species with verrucose thalli containing crystals and rather robust setae, here well represented by *T. amazonum*, *T. carnea*, *T. longispora*, *T. paraguayensis*, and *T. urceolata* (type species). We predict that additional new genera will be distinguished when studying the bulk of non-foliicolous species of *Gyalideopsis* s.lat., which represent various distinctive hyphophore types (Lücking *et al.* 2005). Already the five foliicolous taxa included here formed five unrelated clades, two of which are here recognized as new genera (*Adelphomyces*, *Vezdamyces*).

When comparing previous classifications with our expanded molecular tree (excluding singletons), we confirmed most genera that were already well-defined based on their apothecial and hyphophore or thallus characters, including *Actinoplaca*, *Asterothyrium*, *Aulaxina* s.str., *Caleniopsis*, *Gomphillus*, *Gyalectidium*, *Gyalidea*, and *Rolueckia*. The only exception was the *A. minuta* aggregate that clustered basal to *Caleniopsis* and *Aulaxina* s.str. These genera had also been resolved as well-supported by Lücking *et al.* (2005) when based on phenotype characters alone. There were also several cases of singletons that, while not allowing genus delimitation per se, indicated their separate phylogenetic placement, such as

Arthotheliopsis (distinct from *Aderkomyces*), *Bullatina* and the *Calenia lobulata* group (distinct from *Calenia*), *Gyalideopsis* s.lat. (highly polyphyletic), *Jamesiella* (distinct from *Gyalideopsis* s.lat.), and *Linhartia* and *Psorotheciopsis* (only distantly related to each other). *Jamesiella* was segregated by Lücking *et al.* (2005) from *Gyalideopsis* s.lat. due to the strongly deviating, isidiiform hyphophores dubbed 'thlasidia'; however, due to the lack of non-foliicolous *Gyalideopsis* species in our analysis, nothing can be said about the relationships of *Jamesiella* with these lineages. *Linhartia*, with small ascospores with thin walls and septa, had been variously included in *Psorotheciopsis*, with large ascospores with thick walls and septa, or treated separately from the latter (Santesson 1952; Lücking 1999, 2008; Henssen & Lücking 2002; Aptroot & Lücking 2002). Our analysis suggests that both are separate lineages, but the sampling is very limited and more species and specimens in this group need to be sequenced.

While our analysis did not reveal any new or previously unrecognized synonymies, we propose to recognize 17 lineages at the genus level, four of these with names available, all based on Batista and co-workers (*Microxyphiomyces*, *Psathyromyces*, *Spinomyces*, *Sporocybomyces*; Lücking *et al.* 1998) and the remaining 13 to be described elsewhere (Xavier-Leite *et al.* 2018a). Most of these were predicted as distinct entities or at least suggested to not belonging in the containing genus in a previous cladistic analysis (Lücking *et al.* 2005), namely *Adelphomyces* (*Gyalideopsis epithallina* group), *Aptrootidea* (*Echinoplaca marginata* aggregate), *Bezerroplaca* (*Echinoplaca lucernifera* aggregate), *Caleniella* (*Calenia triseptata* aggregate), *Pseudocalenia* (*Calenia solorinoides* aggregate), *Serusiauxiella* (*Tricharia farinosa* aggregate), *Sipmanidea* (*Echinoplaca neotropica* aggregate), *Verruciplaca* (*Echinoplaca verrucifera* aggregate), and *Vezdamyces* (*Gyalideopsis vulgaris* aggregate). This likewise applies to two of the four reinstated genera based on names established by Batista and co-workers, namely *Microxyphiomyces*, and *Sporocybomyces*.

In contrast, six genera newly distinguished or reinstated in our analysis were not recognized as distinctive groups before: *Aulaxinella* (*Aulaxina minuta* aggregate), nested within *Aulaxina* in Lücking *et al.* (2005); *Batistomyces* (*Tricharia hyalina* aggregate), nested within the *T. vainioi* group; *Monocalenia* (*Calenia monospora* aggregate), nested within *Calenia* s.lat.; *Psathyromyces* (*Aderkomyces heterellus* aggregate), nested within *Aderkomyces*; *Roselvira* (*Aderkomyces purullhensis* aggregate), nested within the *T. vainioi* group; and *Spinomyces* (*Aderkomyces albostrigosus* aggregate), nested within *Aderkomyces* in Lücking *et al.* (2005). *Roselvira* distinguished from *T. vainioi* and relatives by the chroodiscoid apothecia, which were considered of no systematic value by Lücking *et al.*

(2005) but apparently denote distinctive lineages; this is also supported by the position of *Calenia lobulata* separate from other *Calenia* species. The phylogenetic position of *Calenia monospora*, far outside *Calenia* s.lat. and close to *Asterothyrium*, came as a surprise, particularly since the morphologically similar *C. lueckingii* is nested within *Calenia* s.lat. This was one of the very rare instances in which the phenotype was not indicative of genus-level placement. The apparent polyphyly of *Aderkomyces* sensu Lücking *et al.* (2005) further reflects the systematic importance of apothecial morphology, besides chroodiscoid-zeorine also sessile-marginate versus applanate-emarginate.

Unfortunately, several small genera, namely *Aplanocalenia*, *Ferraroa*, *Hippocrepeidea*, *Paratricharia*, and *Phyllogyalidea*, have not yet been molecularly sampled, so their status and phylogenetic relationships cannot be assessed. However, based on our analysis, which supports the predictive value of phenotypic features for the delimitation of genera, due to their strongly derived characters we suggest these taxa to represent good genera. As already outlined above, one further shortcoming of our analysis is that it focused on foliicolous taxa, largely omitting the diversity of non-foliicolous lineages reflected by the genus *Gyalideopsis* s.lat. and its recent segregates (e.g. *Diploschistella* and *Lithogylideopsis*). As suggested by the cladistic analysis of Lücking *et al.* (2005), due to their enormous variation of hyphophore types, these groups might include several additional, unrecognized genera. Clearly, the next step in the study of Gomphillaceae is to focus on these mostly rare and often ephemeral taxa with a high ecological diversity.

While a combination of thallus, apothecial, and hyphophore morphology is highly predictive for genus-level lineages, it is not indicative of phylogenetic placement of genera, suggesting that certain phenotypes evolved several times independently within the family. Increased backbone support is needed to address this question further. On the other hand, there are some indications from certain character combinations of intergeneric relationships. Thus, the close phylogenetic relationship of *Aulaxina* with *Caleniopsis* was predicted based on a similar type of hyphophores, including the hypothesis that the carbonaceous margin in *Aulaxina*, lacking algae, was derived from a thallose margin including algae, rather than representing a proper excipulum (Vězda & Poelt 1987; Lücking 1997; Lücking *et al.* 2005). The level of evolutionary plasticity between closely related genera is otherwise exemplified by the placement of *Gomphillus*, which for a long time had been considered a highly derived, unique and isolated lineage unrelated to the other genera now placed in the family (Watson 1929; Esslinger 1975; Hafellner 1984, 1988) but is apparently related to echinoplacoid lineages, from which it deviates strongly in its vertically elongated apothecia with filiform

ascospores (resembling those of the unrelated genus *Stictis* in Stictidaceae) and its umbelliform hyphophores.

Our analysis rendered most species that were represented by more than one OTU as monophyletic, although in some cases more than one species appear to form a species complex. These instances are in need of further study. In a few cases, names applied to specimens based on phenotype resulted in polyphyletic assemblages. This was particularly obvious in the genus *Gyalectidium*, a taxon originally based in a single species (the other two included species representing unrelated taxa in Pilocarpaceae; Santesson 1952) and subsequently expanded to about 50 species (Ferraro *et al.* 2001). Both phenotypically and molecularly, *Gyalectidium* is a strongly supported clade, characterized by its derived, squamiform hyphophores (Lücking *et al.* 2005). Even if this genus appeared to be rather well studied, particularly with regard to the most abundant species such as *G. filicinum* and *G. imperfectum*, our results suggest a high level of cryptic speciation, also seen in some other genera (*Aulaxinella*, *Serusiauxiella*, *Tricharia* etc.). If this holds true across the family, the current number of 418 accepted species could likely double including disentangling cryptic speciation and also new discoveries to be expected. Notwithstanding, while species concepts are in need of revision in many instances, overall, the phenotype characters used to delimit species or at least species complexes appear to be quite successful to infer genera, as shown by the large proportion of monophyletic clades represented by names applied based on phenotype features.

In conclusion, this study substantially improves our understanding of phylogenetic classification within the family Gomphillaceae, but also points out various aspects for further research, including but not restricted to: (1) increased taxon sampling to include several non-foliicolous species; (2) addition of at least one protein-coding marker (*RPB2*), to attempt to increase backbone resolution to be able to address broader evolutionary questions; and (3) exemplar studies of common, widespread taxa to test for further cases of cryptic speciation and be able to estimate the true species richness in this family.

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) supported the work abroad at the Botanical Garden and Botanical Museum Berlin Berlin (Processo 207282/2015-3), funded the collecting trips (Processo 401186/2014-8), and supported a collaborative project with RL as Special Visiting Professor

(Processo 314570/2014-4), as well as research projects by MESC (Processo 309058/2015-5) and BTG (300982/2016-3). We also thank Dubán Canal for assistance with lab logistics and André Aptroot for collecting additional fresh material from the Amazon and the Netherlands for this work.

5. REFERENCES

- Aptroot, A., Lücking, R. 2002. Proposal to conserve *Gyalidea* (lichenized fungi: Asterothyriaceae, Ostropales) against an additional name, *Solorinella*. *Taxon* 51: 565.
- Aptroot, A., Lücking, R. 2003. Phenotype-based phylogenetic analysis does not support generic separation of *Gyalidea* and *Solorinella* (Ostropales: Asterothyriaceae). *Bibliotheca Lichenologica* 86: 53–78.
- Baloch, E., R. Lücking, H. T. Lumbsch, M. Wedin 2010. Major clades and phylogenetic relationships between lichenized and non-lichenized lineages in Ostropales (Ascomycota: Lecanoromycetes). *Taxon* 59: 1483–1494.
- Batista, A.C. 1961. Um pugilo de gêneros novos de líquens imperfeitos. Publicações, Instituto de Micologia da Universidade do Recife 320: 1-31.
- Batista, A.C., Peres, G.E.P. 1964. Líquens imperfeitos: novos gêneros e espécies de Manaus. Anais do XIV Congresso da Sociedade Botânica do Brasil: 89-102.
- Batista, A.C., Maia, H. da S. 1967. Novos líquens imperfeitos do Amazonas e de Pernambuco. Atas do Instituto de Micologia da Universidade Federal de Pernambuco 5: 55-71. (Publicações, Instituto de Micologia da Universidade do Recife 562).
- Batista, A.C., Poroca, D.J.M. 1970. Uma nova espécie de *Echinoplaca*, da Amazônia. Publicações, Instituto de Micologia da Universidade Federal de Pernambuco 635: 1-8.
- Esslinger, T.L. 1975. A new North American species of the lichen genus *Gomphillus*. *Mycotaxon* 1: 189–192.
- Ferraro, L.I., Lücking, R., Sérusiaux, E. 2001. A world monograph of the lichen genus *Gyalectidium* (Gomphillaceae). *Botanical Journal of the Linnean Society* 137: 311-345.
- Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95-98.
- Hafellner, J. 1984. Studien in Richtung einer natürllicheren Gliederung der Sammelfamilien Lecanoraceae und Lecideaceae. Beiheft zur *Nova Hedwigia* 79: 241–371.
- Hafellner, J. 1988. *Principles of classification and main taxonomic groups*. Pp. 41–52 in M. Galun (ed.), *CRC Handbook of lichenology*, Vol. 3. CRC Press, Boca Raton, FL.

- 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.
- Katoh, K., Asimenos, G., Toh, H. 2009. Multiple Alignment of DNA Sequences with MAFFT. In: Posada, D. (ed.) Bioinformatics for DNA Sequence Analysis. *Methods in Molecular Biology* 537: 39-64.
- Katoh, S. 2013. MAFFT: multiple sequence alignment software version 7: improvements in performance and usability (outlines version 7). *Molecular Biology and Evolution* 30: 772-780.
- 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., E. Sérusiaux, L. C. Maia & E. C. G. Pereira. 1998. A revision of the names of foliicolous lichenized fungi published by Batista and co-workers between 1960 and 1975. *Lichenologist* 30: 121–191.
- Lücking, R., Cáceres, M.E.S., Maia, L.C. 1999. Revisão taxonômica e nomenclatural de líquens foliícolas e respectivos fungos liquenícolas registrados para o estado de Pernambuco, Brasil, por Batista e colaboradores. *Acta Botanica Brasilica* 13: 115–128.
- Lücking, R. 1999. Adiciones y correcciones al conocimiento de la líquenoflora foliícola de Costa Rica. La familia Asterothyriaceae y el género *Chroodiscus* (Thelotremataceae), con un análisis filogenético. *Cryptogamie Mycologie* 20: 193–224.
- 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.
- Lücking, R., Sérusiaux, E., Vězda, A. 2005. Phylogeny and systematics of the lichen family Gomphillaceae (Ostropales) inferred from cladistic analysis of phenotype data. *The Lichenologist* 37: 123-170.
- Lücking, R. 2008. *Foliicolous Lichenized Fungi*. The New York Botanical Garden Press, pp. 873.
- Lücking, R., A. Tehler, F. Bungartz, E. Rivas Plata, H. T. Lumbsch. 2013. Journey from the West: did tropical Graphidaceae (lichenized Ascomycota: Ostropales) evolve from a saxicolous ancestor along the American Pacific coast? *American Journal of Botany* 100: 844–856.

- 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(4): 361-416.
- Papong, K., R. Lücking, A. Thammathaworn, K. Boonpragob. 2008. Four new taxa of *Chroodiscus* (thelotreroid Graphidaceae) from southeast Asia. *Bryologist* 112 (1): 152-163.
- Penn, O., Privman, E., Ashkenazy, H., Landan, G., Graur, D., Pupko, T. 2010a. GUIDANCE: A web server for assessing alignment confidence scores. *Nucl. Acids Res.* 38 (Web Server issue): W23–W28.
- Penn, O., Privman, E., Landan, G., Graur, D., Pupko, T. 2010b. An alignment confidence score capturing robustness to guidetree uncertainty. *Molec. Biol. Evol.* 27: 1759–1767.
- Rivas Plata, E. 2011. Historical Biogeography, Ecology, and Systematics of the Family Graphidaceae (Ascomycota: Ostropales). Ph.D. Dissertation, University of Illinois at Chicago, U.S.A.
- Rivas Plata, E., R. Lücking, H. T. Lumbsch. 2012. A new classification for the lichen family Graphidaceae s. lat. (Ascomycota: Lecanoromycetes: Ostropales). *Fungal Diversity* 52: 107–121.
- Rivas Plata, E., S. Parmen, B. Staiger, A. Mangold, A. Frisch, G. Weerakoon, J. E. Hernández-M., M. E. S. Cáceres, K. Kalb, H. J. M. Sipman, R. S. Common, M. P. Nelsen, R. Lücking, H. T. Lumbsch. 2013. A molecular phylogeny of Graphidaceae (Ascomycota: Lecanoromycetes: Ostropales) including 428 species. *MycKeys* 6: 55–94.
- Sanders, W.B., De Los Ríos, A. 2016. Structure of foliicolous thalli of the Gomphillaceae in a south-western Florida lichen community. *The Lichenologist* 48(4): 293–303.
- Santesson, R. 1952. Foliicolous lichens – A revision of the taxonomy of the obligately foliicolous, lichenized fungi. *Symbiosis Botanical Upsala* 12(1): 1 – 590.
- Sérusiaux, E., De Sloover, J. R. 1986. Taxonomical and ecological observations on foliicolous lichens in northern Argentina, with notes on the hyphophores of Asterothyriaceae. *Veröffentlichungen des Geobotanischen Instituts, Stiftung Rübel, Zürich* 91: 260–292.
- Sérusiaux, E. 1997. *Sporodiopsis*, a new genus of lichens (Ectolechiaceae) from S–E Asia. *Abstracta Botanica* 21(1): 145–152.
- Vězda, A. 1973. Foliicole Flechten aus der Republik Guinea (W.–Afrika). I. *Acta Musei Silesiae, Opava* 22: 67–90.

- Vězda, A. 1979. Flechtensystematische Studien. XI. Beiträge zur Kenntnis der Familie Asterothyriaceae (Discolichenes). *Folia Geobotanica et Phytotaxonomica, Praha* 14: 43–94.
- Vězda, A., Poelt, J. 1987. Flechtensystematische Studien. XII. Die Familie Gomphillaceae und ihre Gliederung. *Folia Geobotanica et Phytotaxonomica, Praha* 22:179–198.
- Vilgalys, R., Hester, M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* 172: 4238-4246.
- Watson, W. 1929. The classification of lichens. *New Phytologist* 28: 1–116.
- 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): 032–040.
- Zhou, S., Stanosz, G. R. 2001. Primers for amplification of mt SSU rDNA, and a phylogenetic study of *Botryosphaeria* and associated anamorphic fungi. *Mycological Research* 105: 1033-1044.

Capítulo 2

New genera in the lichenized family Gomphillaceae (Ascomycota: Ostropales) utilizing Integrative Taxonomy

**New genera in the lichenized family Gomphillaceae (Ascomycota: Ostropales) utilizing
Integrative Taxonomy**

Amanda Barreto Xavier-Leite^{1,5}, Bruno Tomio Goto², Robert Lücking³ and Marcela E. da
Silva Cáceres⁴

¹ *Programa de Pós-Graduação em Sistemática e Evolução, CB, Universidade Federal do Rio Grande do Norte, Campus Universitário, 59072-970, Natal, RN, Brazil;* ² *Departamento de Botânica e Zoologia, CB, Universidade Federal do Rio Grande do Norte, Campus Universitário, 59072-970, Natal, RN, Brazil;* ³ *Botanischer Garten und Botanisches Museum, Freie Universität Berlin, Königin-Luise-Strasse 6–8, 14195 Berlin, Germany;* ⁴ *Departamento de Biociências, Universidade Federal de Sergipe, CEP: 49500-000, Itabaiana, Sergipe, Brazil*

ABSTRACT

Molecular phylogenetic analysis in comparison with phenotype characters of Gomphillaceae indicated the existence of a total of 38 genus-level clades in the studied subset of taxa, 17 of which in need to be newly recognized as formal genera. Four of these are reinstated genus names, including one validation, namely *Microxyphiomyces* Bat., Valle & Peres, *Psathyromyces* Bat. & Peres, *Spinomyces* Bat. & Peres ex Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, and *Sporocybomyces* H. Maia. The remaining 13 are newly described: *Adelphomyces* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Aptrootidea* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Aulaxinella* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Batistomyces* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Bezerroplaca* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Caleniella* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Monocalenia* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Pseudocalenia* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Roselviria* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Serusiauxiella* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Sipmanidea* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, *Verruciplaca* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*, and *Vezdomyces* Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*. The following 53 new combinations are introduced for the species included in the new and reinstated genera: *Adelphomyces cochlearifer* (Lücking & Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb.*

⁵ Corresponding author's e-mail: amandabxleite@hotmail.com

nov., *A. epithallina* (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *A. parvula* (Hafellner & Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *Aptrootidea amapensis* (Bat. & Poroca) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *A. atrofusca* (R. Sant.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *A. atromuralis* (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *A. marginata* (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *A. triseptata* (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *A. wilsoniorum* (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *Aulaxinella corticola* (Kalb & Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *A. minuta* (R. Sant.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *A. multiseptata* (R. Sant.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *Basistomyces pallidus* (Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *B. hyalinus* (Kalb & Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *Bezerroplaca fusconitida* (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *B. incrustatociliata* (Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *B. lucernifera* (Kalb & Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *B. pachyparaphysata* (R. Sant.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *B. streimannii* (Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *Caleniella maculans* (Vain.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *C. triseptata* (Zahlbr.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *Microxyphiomyces cuneatus* (L.I. Ferraro & Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *M. demoulinii* (Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *M. elegans* (Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *M. kashiwadani* (G. Thor, Lücking & Tat. Matsumoto) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *M. lancicarpus* (Kalb & Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *M. manaosensis* Bat., Valle & Peres. = *M. vainioi* (R. Sant.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *M. santessonianus* (Kalb & Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *M. santessonii* (D. Hawks.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *M. similis* (Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *M. variratae* (Lücking & Sipman) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *Monocalenia monospora* (Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *Psathyromyces planus* (Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *P. heterellus* (Stirt.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *Pseudocalenia solorinoides* (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *Roselviria lobulimarginata* (Sipman & Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *R. purulhensis* (Lücking, Sérus. & Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *Serusiaxiella farinosa* (R. Sant.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *Sipmanidea neotropica* (Lücking) Xavier-Leite, M. Cáceres

& Lücking, *comb. et stat. nov.*, *Spinomyces aggregatus* (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. et stat. nov.*, *S. albostrigosus* (Lücking, Sérus. & Vězda) Xavier-Leite, Cáceres & Lücking, *comb. nov.*, *S. deslooveri* (Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *S. guatemalensis* (Lücking & Barillas) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *S. microcarpus* (Etayo & Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *S. verrucosus* (Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *Sporocybomyces leucomuralis* (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *S. leucotrichoides* (Vain.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *S. macgregorii* (Vain.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *Verruciplaca calcarea* (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. et stat. nov.*, *V. furcata* (Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*, *V. verrucifera* (Lücking) Xavier-Leite, Cáceres & Lücking, *comb. nov.*, *Vezdamyces albopruinosus* (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. et stat. nov.*, and *V. vulgaris* (Müll. Arg.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*

Keywords. Batista, Foliiicolous lichens, mitochondrial small subunit rDNA, mtSSU, nuclear large subunit rDNA, nuLSU, morphological data, nomenclature

1. INTRODUCTION

The family Gomphillaceae was originally based on the single, monospecific genus *Gomphillus* Nyl. (Watson 1929), described by Nylander (1855). The bulk of the genera later included in this family were largely classified in a separate family, Asterothyriaceae, also established by Watson (1929) but more precisely defined by Santesson (1952). The latter author recognized six genera in Asterothyriaceae, namely *Asterothyrium* Müll. Arg., *Calenia* Müll. Arg., *Echinoplaca* Fée (including *Actinoplaca* Müll. Arg.), *Gyalectidium* Müll. Arg., *Psorotheciopsis* Rehm (including *Linhartia* Sacc. & P. Syd.), and *Tricharia* Fée. This group partly corresponded to Ectolechiaceae sensu Vainio (1896) and Zahlbruckner (1907), but the generic type of that family, *Sporopodium* Mont., was found to be unrelated to the above genera, belonging in Lecanorales, and so Asterothyriaceae was adopted by Santesson (1952) to accommodate these genera. In addition, Santesson (1952) recognized a further genus, *Aulaxina* Fée, in Graphidaceae.

Until to Santesson's (1952) monograph, it had not been recognized that *Gomphillus* and several genera placed in Asterothyriaceae shared a unique type of conidial anamorph, with the conidia formed externally on supporting structures as multiseptate, filamentous hyphal

threads or moniliform chains. Müller (1891) first described these for *Actinoplaca* (= *Echinoplaca*) *strigulacea* Müll. Arg., as so-called 'sporodochia', whereas Santesson (1952) considered the squamiform conidial anamorph formed by *Gyalectidium filicinum* Müll. Arg. as a lichenicolous fungus, *Cristidium pallidum* R. Sant. Shortly after Santesson's (1952) monograph, during a period of more than a decade starting in the late 50s, the Brazilian mycologist Augusto Chaves Batista and his collaborators described a larger number of new genera based on conidial anamorphs corresponding to Asterothyriaceae and Gomphillaceae (Batista 1961; Batista & Peres 1964; Batista & Maia 1967; Batista & Poroca 1970). These were later mostly established as synonyms of existing genera (Lücking *et al.* 1998, 1999), namely: *Aciesia* Bat. (= *Tricharia*), *Actinoteichus* Cavalc. & Poroca (= *Asterothyrium*), *Aderkomyces* Bat. (= *Tricharia*), *Lochomyces* Bat. nom. inval. (= *Aulaxina*), *Microxyphiomyces* Bat., Valle & Peres (= *Tricharia*), *Phallomyces* Bat. & Valle (= *Echinoplaca*), *Psathyromyces* Bat. & Peres (= *Tricharia*), *Setomyces* Bat. & Peres nom. inval. (= *Tricharia*), *Spinomyces* Bat. & Peres nom. inval. (= *Echinoplaca* or *Tricharia*), *Sporocybomyces* H. Maia (= *Echinoplaca*), *Tauromyces* Cavalc. & A. A. Silva (= *Gyalectidium*), and *Tegoa* Bat. & Peres nom. inval. (= *Asterothyrium*).

Up to this time, the genus *Gomphillus* and the family Gomphillaceae had not been connected to Asterothyriaceae. While describing a new species, *G. americanus* Essl., Esslinger (1975) discussed the systematic position of the genus, which in the past had variously been related to Cladoniaceae or Lecideaceae (Duby 1830; Nylander 1855, 1860; Zahlbruckner 1905; Poelt 1973; Henssen & Jahns 1974). Esslinger (1975) concluded that *Gomphillus* had no close relatives in Lecideaceae and that placement in a family of its own remained warranted.

The picture changed entirely when Vězda (1973) first recognized the true nature of the conidial anamorphs of these lichen fungi, calling them hyphophores. Based on this finding, Vězda (1979) proposed that *Gomphillus* was closely related to the genera treated in Asterothyriaceae by Santesson (1952) and consequently included *Gomphillus* and the additional genera *Aulaxina*, *Gyalidea* Lettau ex Vězda, *Gyalideopsis* Vězda, *Linhartia*, and *Solorinella* Anzi in an broadly emended Asterothyriaceae, for the first time delimiting this group in its natural sense. Later, Vězda & Poelt (1987) proposed to reinstate Gomphillaceae for the genera producing hyphophores and with anastomosing paraphyses, whereas Asterothyriaceae was retained for genera lacking hyphophores and with unbranched paraphyses. Shortly thereafter, Vězda & Poelt (1990) also separated *Gyalidea*, *Linhartia*, and *Solorinella* in its own family, Solorinellaceae, while *Asterothyrium* had been related to

Thelotremataceae (Vězda & Poelt 1987). However, Asterothyriaceae was retained to include *Asterothyrium*, *Gyalidea* (= *Solorinella*), and *Psorotheciopsis* (= *Linhartia*) in most subsequent treatments (Lücking 1997, 1999, 2008). Notably, Hafellner (1984) argued that *Asterothyrium* and *Gomphillus*, as the type genera of the two families in question, could not be related, and later proposed to assign Gomphillaceae to its own order, Gomphillales (Hafellner 1988).

While the first molecular study on this group demonstrated that Asterothyriaceae and Gomphillaceae are closely related and form a monophyletic lineage in the order Ostropales (Lücking *et al.* 2004), the taxon sampling at the time was too limited to address genus delimitations particularly in the Gomphillaceae. Since the few genera in Asterothyriaceae appeared to be rather well defined (Lücking 1999; Henssen & Lücking 2002), Lücking *et al.* (2005) performed a broad-scale, phenotype-based cladistic study on all species assigned to Gomphillaceae, to test the genus concept applied at the time, including additional genera that had been established in the meanwhile. Besides the genera already distinguished at the time of Santesson's monograph (1952), namely *Aulaxina* (= *Lochomyces*), *Calenia* (= *Bullatina* Vězda & Poelt), *Echinoplaca* (= *Spinomyces* p.p., *Sporocybomyces*), *Gomphillus*, *Gyalectidium* (= *Cristidium*, *Tauromyces*), and *Tricharia* (= *Microxyphiomyces*, *Setomyces*, *Spinomyces* p.p.), the subsequently established genera *Caleniopsis* Vězda & Poelt, *Gyalideopsis* (= *Epilithia* Nyl., *Microlychnus* A. Funk, *Microspatha* P. Karst.), *Hippocrepidea* Sérus., and *Paratracharia* Lücking, were included in this analysis. Lücking *et al.* (2005) further reinstated some older names, including some of those established by Batista and co-workers, namely *Actinoplaca*, *Aderkomyces* (= *Psathyromyces*), *Arthotheliopsis* Vain. (= *Phallomyces*), and *Diploschistella* Vain. In addition, five genera were newly described: *Aplanocalenia* Lücking, Sérus. & Vězda, *Ferraroa* Lücking, Sérus. & Vězda, *Jamesiella* Lücking, Sérus. & Vězda, *Lithogyalideopsis* Lücking, Sérus. & Vězda, and *Rubrotricha* Lücking, Sérus. & Vězda.

After further molecular studies supported the notion that Asterothyriaceae was nested within Gomphillaceae and the two families should therefore be merged under Gomphillaceae, the number of genera raised to 24, with a total of 418 species (Lücking *et al.* 2017): *Actinoplaca* Müll. Arg., *Aderkomyces* Bat., *Aplanocalenia* Lücking, Sérus. & Vězda, *Arthotheliopsis* Vain., *Asterothyrium* Müll. Arg., *Aulaxina* Fée, *Calenia* Müll. Arg., *Caleniopsis* Vězda & Poelt, *Diploschistella* Vain., *Echinoplaca* Fée, *Ferraroa* Lücking, Sérus. & Vězda, *Gomphillus* Nyl., *Gyalectidium* Müll. Arg., *Gyalidea* Lettau ex Vězda, *Gyalideopsis*, *Hippocrepidea* Sérus., *Jamesiella* Lücking, Sérus. & Vězda, *Lithogyalideopsis*

Lücking, Sérus. & Vězda, *Paratracharia* Lücking, *Phyllogyalidea* Lücking & Aptroot, *Psorotheciopsis* Rehm, *Rolueckia* Papong, Thammath. & Boonpr., *Rubrotricha* Lücking, Sérus. & Vězda, and *Tricharia* Fée. As part of the present work, a broad taxon sampling focusing on foliicolous lineages and using two molecular markers (mtSSU and nuLSU) tested this classification and found that several of these genera were still polyphyletic, particularly *Aderkomyces*, *Aulaxina*, *Calenia*, *Echinoplaca*, and *Tricharia*, distinguishing at least an additional 17 lineages that deserved recognition at genus status (Xavier-Leite *et al.* 2018a). While four of these have names available (one in need to be validated), here we establish the following 13 new genera for the remaining lineages: *Adelphomyces*, *Aptrootidea*, *Aulaxinella*, *Batistomyces*, *Bezerroplaca*, *Caleniella*, *Monocalenia*, *Pseudocalenia*, *Roselviria*, *Serusiaxiella*, *Sipmanidea*, *Vezdamyces*, and *Verruciplaca*.

2. MATERIALS AND METHODS

The emended generic classification proposed here was based on our simultaneously published two-locus phylogeny (Xavier-Leite *et al.* 2018a). Since the topology for the entire family remained unresolved in some parts and also absent data on the bulk of non-foliicolous *Gyalideopsis* s.lat. and its relatives, we formally recognized new genera (or reinstated previous names) when three criteria were more or less fulfilled: (1) including of the lineage in another genus would render that genus polyphyletic and potential monophyly could be rejected based on tests using topological constraints (SH test in RAxML 8.2.0; Stamatakis 2014); (2) the lineage was monophyletic and supported with at least 70% bootstrap support, whereas there was lack of support of its stem node with the most closely related clade and/or the stem node(s) were comparatively long; and (3) there was correlation with diagnostic phenotype features. For the latter, in a separate study (Xavier-Leite *et al.* 2018b) we employed phenotype-based phylogenetic binning to assign species with lack of molecular data to molecularly defined clades and then evaluated phenotype variation within each clade, while largely defining the clade based on its included sequenced species.

For each genus thus newly delimited below, we provide a brief diagnosis and a more detailed description, as well as images of representative species and features.

3. RESULTS AND DISCUSSION

The new and reinstated genera.

Adelphomyces Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*

MycoBank MB 000000

Fig. 1

Type species: *Adelphomyces epithallina* (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Gyalideopsis epithallina* Lücking. *Biblioth. Lichenol.* 65: 66 (1997).

Diagnosis: Lichenicolous; apothecia sessile, biatorine (*Gyalideopsis* type); ascospores very small, 1–3-septate; hyphophores (when known) setiform, black, apically widened (rostrate or spathulate); diahyphae moniliform.

Etymology: The generic name refers to the lichenicolous growth of two of the three species on thalli of species of the same family, Gomphillaceae; in adelphoparasites, the host is closely related to the parasite.

Genus description: Lichenicolous on species of Gomphillaceae (two species) or Pilocarpaceae (one species). Apothecia sessile, biatorine, with distinct margin. Excipulum hyphal but hyphae densely arranged. Hypothecium prosoplectenchymatous, pale. Epithecium indistinct. Ascospores very small, 1–3-septate. Hyphophores where known setiform, black, apically widened and either rostrate or spathulate. Diahyphae inserted apically, branched throughout, moniliform, segments ellipsoid to drop-shaped, colorless.

Discussion: The species assigned to this new genus were previously included in *Gyalideopsis* s.lat., which based on cladistic and molecular phylogenetic analyses (Lücking *et al.* 2004, 2005; Xavier-Leite *et al.* 2018a) is a highly polyphyletic assemblage. In a previous cladistic analysis, the clade including the three lichenicolous species was strongly supported (Lücking *et al.* 2005) and therefore, together with the placement of the type species separate from other representatives of *Gyalideopsis* in our molecular analysis (Xavier-Leite *et al.* 2018a), we include the two non-sequenced taxa in this genus. Besides their lichenicolous growth habit, the species of this genus are recognized by their *Gyalideopsis*-type, sessile, yet very small apothecia in combination with their very small ascospores with few septa.

Additional species included (see Xavier-Leite *et al.* 2018b):

Adelphomyces cochlearifer (Lücking & Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Gyalideopsis cochlearifera* Lücking & Sérus. [as '*cochlearifer*'], *Lichenologist* 30: 543 (1998).

Adelphomyces parvula (Hafellner & Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Gyalideopsis parvula* Hafellner & Vězda in Kalb & Vězda, *Biblioth. Lichenol.* 29: 43 (1988).

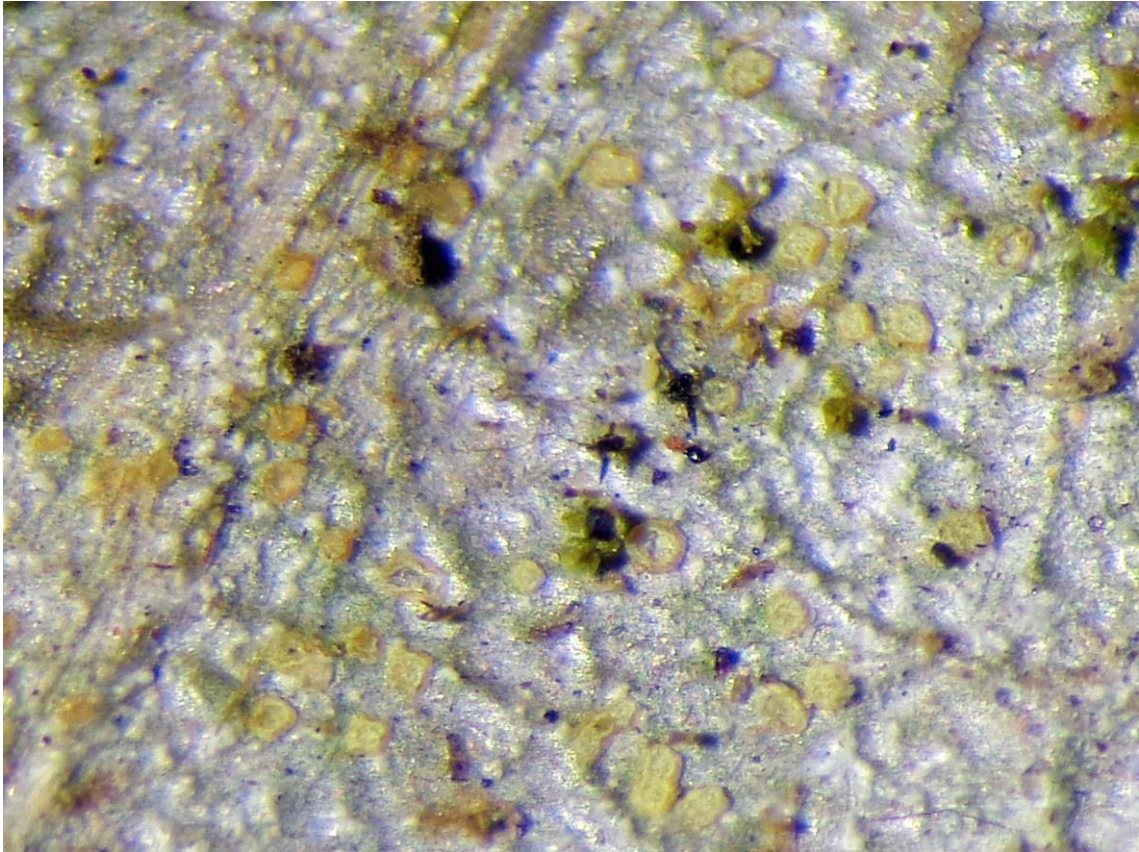


Figure 1: New genus *Adelphomyces*, sequenced specimen. *Adelphomyces epithallinus*, Brazil [23107].

Aptrootidea Xavier-Leite, M. Cáceres & Lüicking, *gen. nov.*

MycoBank MB 000000

Fig. 2 (A-F), Fig. 3 (A-D)

Type species: *Aptrootidea marginata* (Lüicking) Xavier-Leite, Cáceres & Lüicking, *comb. nov.* [MycoBank MB 000000]. Basionym: *Echinoplaca marginata* Lüicking. *Biblioth. Lichenol.* 65: 57 (1997).

Diagnosis: Lichenized; often with sterile, short, dart setae on translucent prothallus; apothecia adnate to erumpent, thinly zeorine to emarginate (*Echinoplaca* type), brown to brown-black; ascospores variable; hyphophores unknown.

Etymology: This new genus is dedicated to our colleague and friend, André Aptroot, for his numerous contributions to tropical lichenology.

Genus description: Thallus foliicolous, continuous or dispersed, uneven to verrucose, lacking or with short, dark setae usually formed on a translucent prothallus. Apothecia adnate (to erumpent), spot-like; disc chocolate-brown to brown-black; proper margin absent, in the

type species often with a thin thalline margin. Excipulum hyphal. Hypothecium prosoplectenchymatous, pale. Epithecium (dark) brown. Ascospores variably septate. Hyphophores unknown.

Discussion: The genus as here defined is likely heterogeneous, including the type species (the only sequenced species) and a group five further species supported to be closely related to the type based on phylogenetic binning (Xavier-Leite *et al.* 2018b). *Echinoplaca marginata* was already recognized as distinct from other *Echinoplaca* species when it was described (Lücking 1997), and therefore its separate placement based on molecular phylogeny (Xavier-Leite *et al.* 2018a) did not come as a surprise. The other five species are included here provisionally based on the binning result; they were already recognized as a separate clade by Lücking *et al.* (2005) based on a cladistic analysis and they likely form an additional, separate genus, but none of the species has been sequenced yet.

Additional species included (see Xavier-Leite *et al.* 2018b):

Aptrootidea amapensis (Bat. & Poroca) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Echinoplaca amapensis* Bat. & Poroca, Publicações. Instituto de Micologia da Universidade de Pernambuco 635: 4 (1970).

Aptrootidea atrofusca (R. Sant.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Echinoplaca atrofusca* R. Sant., Symb. Bot. Upsal. 12(1): 371 (1952).

Aptrootidea atromuralis (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Echinoplaca atromuralis* Lücking, Fl. Neotrop. Monogr. 103: 492 (2008).

Aptrootidea triseptata (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Echinoplaca triseptata* Lücking, Biblioth. Lichenol. 65: 61 (1997).

Aptrootidea wilsoniorum (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Echinoplaca wilsoniorum* Lücking, Fl. Neotrop. Monogr. 103: 491 (2008).

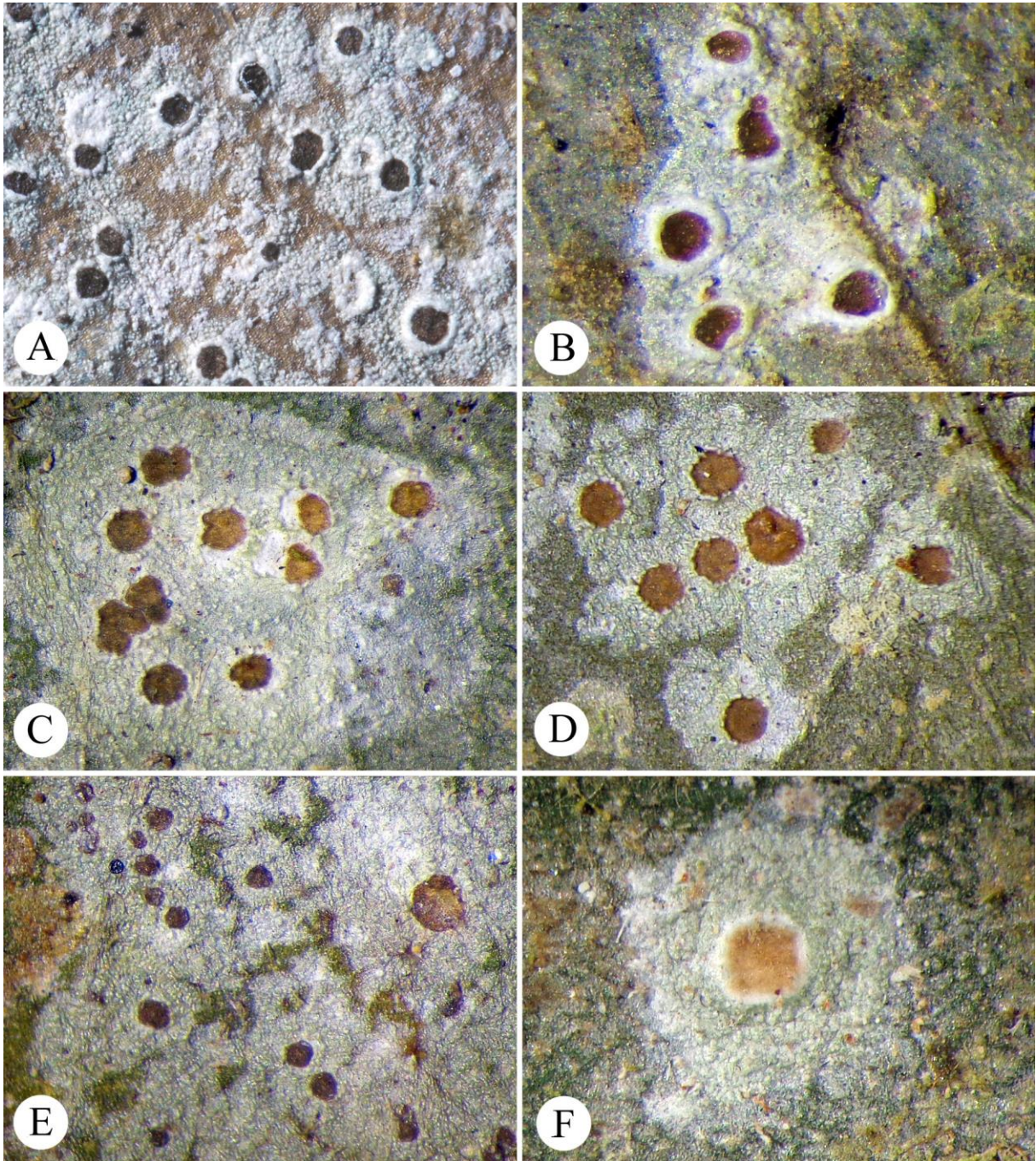


Figure 2: New genus *Aptrootidea*, including sequenced specimens. **A.** *Aptrootidea marginata*, Costa Rica. **B.** *A. marginata*, Brazil [23012]. **C.** *A. marginata*, Brazil [23114]. **D.** *A. marginata*, Brazil [23015]. **E.** *A. marginata*, Brazil [23013]. **F.** *Aptrootidea* sp. nov., Brazil [22024].

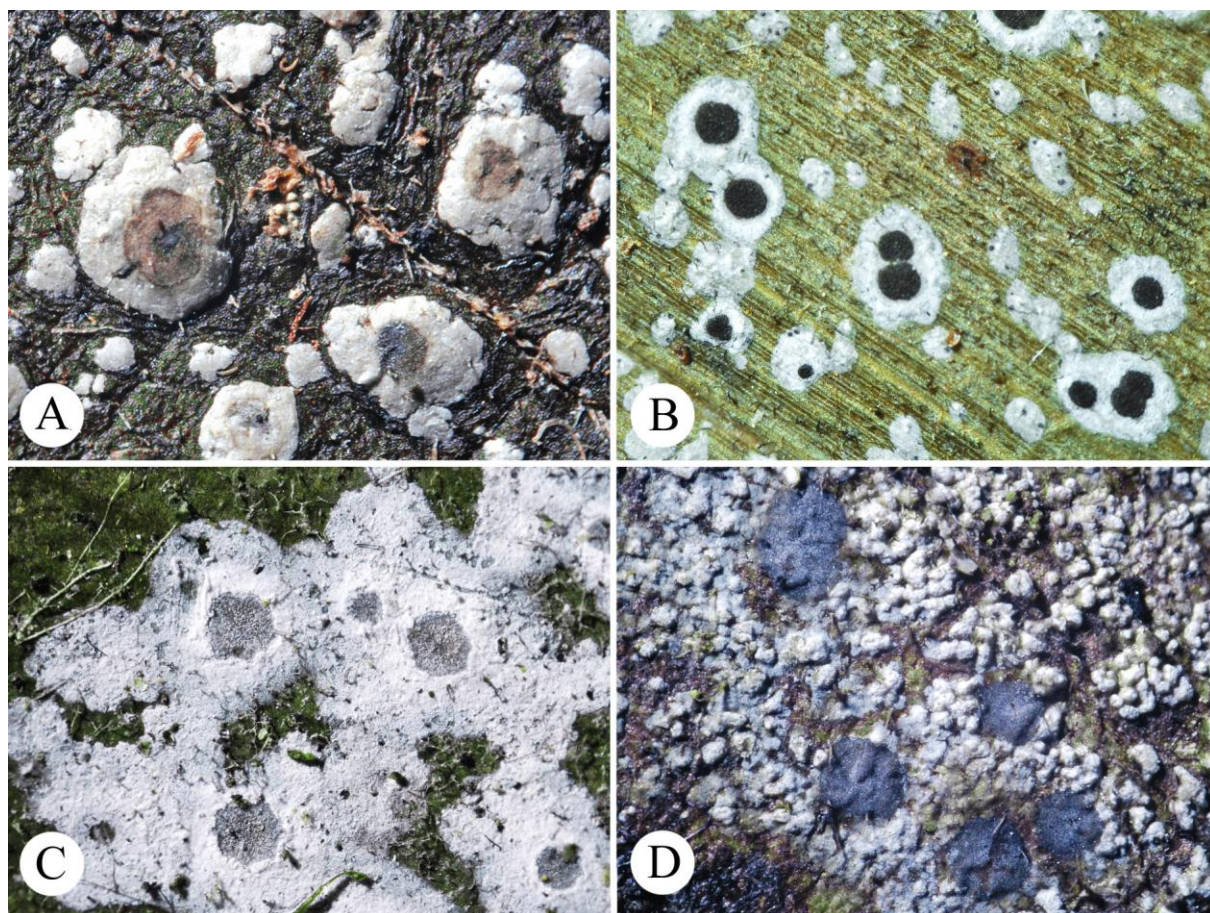


Figure 3: New genus *Aptrootidea*. **A.** *Aptrootidea amapensis*, Brazil. **B.** *A. atrofusca*. **C.** *A. atomuralis*, Costa Rica. **D.** *A. triseptata*, Costa Rica.

Aulaxinella Xavier-Leite, M. Cáceres & Lüicking, *gen. nov.*

MycoBank MB 000000

Fig. 4 (A-F)

Type species: *Aulaxinella minuta* (R. Sant.) Xavier-Leite, Cáceres & Lüicking, *comb. nov.* [MycoBank MB 000000]. Basionym: *Aulaxina minuta* R. Sant., *Symb. Bot. Upsal.* 12(1): 298 (1952).

Diagnosis: Lichenized; thallus continuous, with dark brown prothallus; apothecia erumpent, zeorine with carbonized thalline margin lacking algae (*Aulaxina* type); ascospores variable; hyphophores setiform, black, formed in groups on algal-free thallus patches; diahyphae palmate.

Etymology: The generic name is derived from the closely related genus *Aulaxina*, in which the type species was previously placed, together with the notion that the thalli and apothecia in the type species are comparatively small.

Genus description: Thallus foliicolous, rarely corticolous, continuous, with dark brown prothallus, lacking sterile setae. Apothecia erumpent, zeorine, crater-like; disc brownish; proper margin indistinct, thalline margin distinct, strongly prominent, carbonized, lacking algae. Excipulum prosoplectenchymatous. Hypothecium prosoplectenchymatous, colorless. Epithecium indistinct. Ascospores variably septate. Hyphophores produced in groups on algal-free thallus patches, setiform with blunt apex, black. Diahyphae inserted apically, palmate, in 3–5 separate bunches, emerging from thicker hypha, moniliform, segments ellipsoid, partly 1-septate.

Discussion: Due to the unique combination of thallus, apothecial and hyphophore features, *Aulaxina* was considered one of the most well-delimited genera in this group and its circumscription was never questioned previously (Santesson 1952; Vězda 1979; Vězda & Poelt 1987; Lücking 1997, 2008; Lücking *et al.* 2005). Our molecular phylogenetic analysis demonstrated the genus to be polyphyletic, with *Caleniopsis* positioned inbetween the *Aulaxina minuta* aggregate and *Aulaxina* s.str. *Caleniopsis* differs from *Aulaxina* s.lat. in the uncarbonized apothecia with thicker, distinctly zeorine margin (*Calenia* type). Theoretically, *Caleniopsis* could be included in an emended *Aulaxina* to retain the *A. minuta* aggregate in that genus, but would not reflect the molecular topology, since both the *A. minuta* aggregate and *Caleniopsis* form comparatively long branches, and while *Caleniopsis* is supported as sister to *Aulaxina* s.str., the placement of the *A. minuta* aggregate basal to this assemblage is not supported (Xavier-Leite *et al.* 2018a). In addition, while this alternative solution would resolve the problem of separating the *A. minuta* aggregate from the very similar *Aulaxina* s.str., it would generate the new problem of merging a morphologically distinct entity (*Caleniopsis*) with *Aulaxina*. Therefore, and since the *A. minuta* aggregate can be characterized by a phenotype character (continuous thallus with dark prothallus versus dispersed thallus with translucent prothallus in *Aulaxina* s.str.), we prefer to recognize this clade as a separate genus.

Additional species included (see Xavier-Leite *et al.* 2018b):

Aulaxinella corticola (Kalb & Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Aulaxina corticola* Kalb & Vězda, *Biblioth. Lichenol.* 29: 15 (1988).

Aulaxinella multiseptata (R. Sant.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Aulaxina multiseptata* R. Sant., *Symb. Bot. Upsal.* 12(1): 302 (1952).

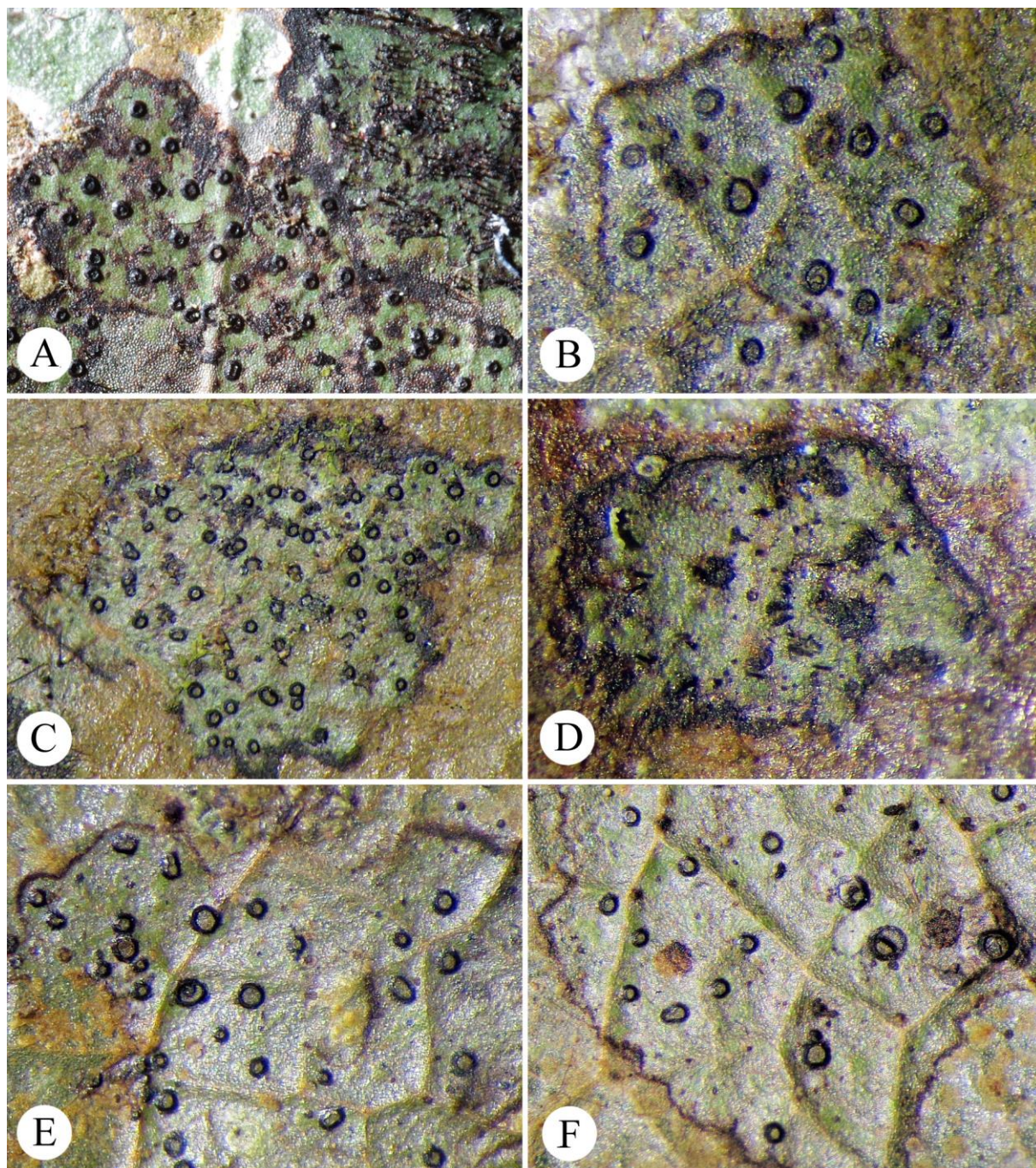


Figure 4: New genus *Aulaxinella*, including sequenced specimens. **A.** *Aulaxinella minuta*, Ecuador. **B.** *A. aff. minuta*, Brazil [23079]. **C.** *A. aff. minuta*, Brazil [23092]. **D.** *A. aff. minuta*, Brazil [22173]. **E.** *A. minuta*, Brazil [22186]. **F.** *A. minuta*, Brazil [22187].

Batistomyces Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*

Mycobank MB 000000

Fig. 5 (A-D)

Type species: *Batistomyces hyalinus* (Kalb & Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia hyalina* Kalb & Vězda. *Biblioth. Lichenol.* 29: 65 (1988).

Diagnosis: Lichenized; thallus continuous, with numerous, dense, short and stiff, black setae; apothecia sessile to substipitate, biatorine, translucent; ascospores variable; hyphophores setiform, black; diahyphae moniliform.

Etymology: This new genus is dedicated to the Brazilian mycologist Augusto Chaves Batista, for his pioneering contributions to the knowledge of tropical fungi and lichens in Brazil, especially in Gomphillaceae.

Genus description: Thallus foliicolous, continuous, with numerous, densely arranged, short, sterile black setae. Apothecia sessile to almost stipitate, biatorine, translucent; proper margin thin, prominent. Excipulum paraplectenchymatous, colorless. Hypothecium colorless. Epithecium indistinct. Ascospores muriform. Hyphophores setiform, black. Diahyphae inserted apically, moniliform, segments sausage-shaped.

Discussion: The genus *Tricharia* was considered by Lücking et al. (2005) to comprise two potentially distinct lineages, *Tricharia* s.str. with verrucose thalli and large and robust setae, and the *T. vainioi* group, with smooth thalli and more delicate setae. This distinction was supported by our molecular analysis (Xavier-Leite *et al.* 2018a), but while *T. hyalina* was considered to belong in the *T. vainioi* group, molecularly it resulted unrelated to that clade or *Tricharia* s.str., and a new genus is required to accommodate this topology. *Tricharia hyalina* was recognized to differ from *T. vainioi* and relatives by the very densely arranged, short and stiff setae (Lücking 2008), and this character might provide a potential synapomorphy, but more taxa in the *T. vainioi* group need to be sequenced to test this assumption.

Additional species included (see Xavier-Leite *et al.* 2018b):

Batistomyces pallidus (Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia pallida* Vězda, *Folia Geobot. Phytotax.* 14: 73 (1979).

Bezerroplaca Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*

MycoBank MB 000000

Fig. 6 (A-F)

Type species: *Bezerroplaca lucernifera* (Kalb & Vězda) Xavier-Leite, Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Echinoplaca lucernifera* Kalb & Vězda, *Biblioth. Lichenol.* 29: 24 (1988).

Diagnosis: Lichenized; thallus continuous, verrucose, with scattered, white setae; apothecia adnate, emarginate (*Echinoplaca* type), brown-black; ascospores muriform; hyphophores setiform, white with darkened apex, with bell-shaped, ciliate diahyphal bunches; diahyphae filiform with spermatozoid terminal segments.

Etymology: This new genus is dedicated to our colleague and friend, Dr. José Luiz Bezerra, for his contributions to the knowledge of Brazilian foliicolous lichens.

Genus description: Thallus foliicolous, usually continuous, finely verrucose, with scattered, sterile white setae. Apothecia adnate and spot-like, emarginate; disc plane, brown-black. Excipulum hyphal, colorless. Hypothecium brown. Epithecium brown. Ascospores muriform. Hyphophores setiform, white but apically darkened. Diahyphae inserted apically, forming bell-shaped, superficially ciliate bunches, filiform but peripheral hyphae thickened and terminal segments narrowly spermatozoid.

Discussion: This new genus was previously recognized as a distinct group (Lücking 1997; Lücking *et al.* 2005), suggesting that *Echinoplaca* s.lat. is polyphyletic and demonstrating that a combination of thallus, apothecial, and hyphophore morphology is diagnostic for genus-level lineages in the family. *Bezerroplaca* is particularly characterized by the bell-shaped diahyphal bunches and the filiform diahyphae with spermatozoid end segments, but also the thallus and apothecial morphology is quite uniform in this group.

Additional species included (see Xavier-Leite *et al.* 2018b):

Bezerroplaca fusconitida (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Echinoplaca fusconitida* Lücking, *Biblioth. Lichenol.* 65: 51 (1997).

Bezerroplaca incrustatociliata (Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Echinoplaca incrustatociliata* Sérus. in Aptroot *et al.*, *Biblioth. Lichenol.* 64: 58 (1997).

Bezerroplaca pachyparaphysata (R. Sant.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Echinoplaca pachyparaphysata* R. Sant., *Symb. Bot. Upsal.* 12(1): 373 (1952).

Bezerroplaca streimannii (Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Echinoplaca streimannii* Sérus. in Aptroot *et al.*, *Biblioth. Lichenol.* 64: 59 (1997).

Caleniella Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*

MycoBank MB 000000

Fig. 7 (A-B)

Type species: *Caleniella triseptata* (Zahlbr.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Calenia triseptata* Zahlbr., Denkschr. Kaiserl. Akad. Wiss. Wien Math.-Naturwiss. Kl. 83: 121 (1909).

Diagnosis: Lichenized; thallus continuous, verrucose, lacking setae; apothecia erumpent, zeorine (*Calenia* type); ascospores small, 3-septate; hyphophores unknown.

Etymology: The name is derived from the name *Calenia*, in which the type species was previously placed, together with the notion that the apothecia in the type species are comparatively small.

Genus description: Thallus foliicolous, continuous, lacking setae. Apothecia erumpent, zeorine; disc pale; proper margin indistinct, thalline margin distinct, strongly prominent, white. Excipulum prosoplectenchymatous, colorless. Hypothecium prosoplectenchymatous, colorless. Epithecium indistinct. Ascospores usually 8 per ascus, 3-septate. Hyphophores unknown.

Discussion: *Calenia* is one of the larger genera in Gomphillaceae that was suspected to be heterogeneous (Lücking 1997; Lücking *et al.* 2005) and our molecular data confirmed this (Xavier-Leite *et al.* 2018a). *Calenia triseptata* was found to be closely related to *Caleniopsis* and *Aulaxina*, although it strongly differs in thallus and apothecial morphology and lacks hyphophores. Establishment of a new genus for this clade is therefore warranted. The main difference with *Calenia* s.str., which is not closely related, is found in the small, 3-septate ascospores.

Additional species included (see Xavier-Leite *et al.* 2018b):

Caleniella maculans (Vain.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Asterothyrium maculans* Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 170 (1921); *Calenia maculans* (Vain.) R. Sant., Symb. Bot. Upsal. 12(1): 343 (1952).

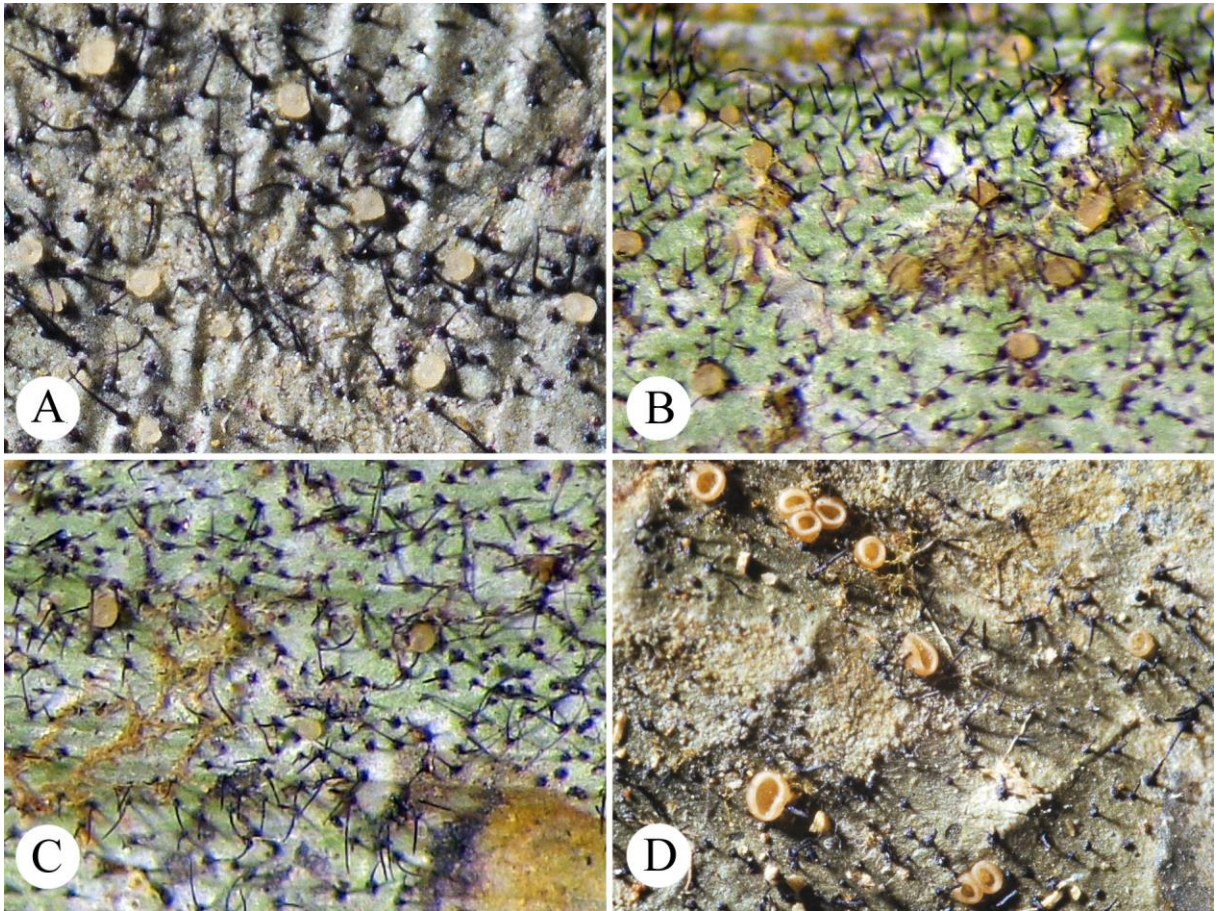


Figure 5: New genus *Batistomyces*, including sequenced specimens. **A.** *Batistomyces hyalinus*, French Guiana. **B.** *B. hyalinus*, Brazil [23154]. **C.** *B. hyalinus*, Brazil [23155]. **D.** *B. pallidus*, holotype.

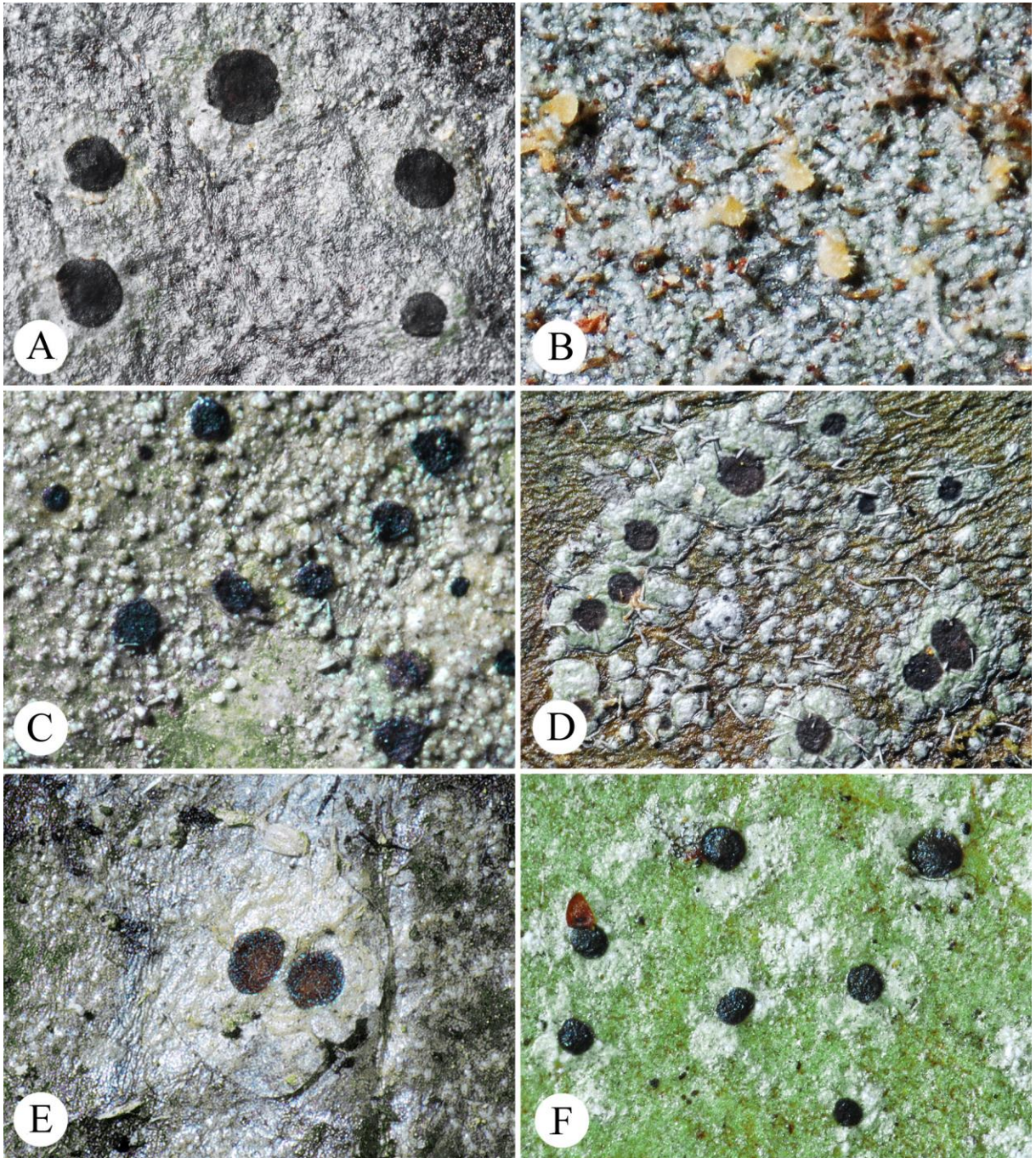


Figure 6: New genus *Bezerroplaca*. **A.** *Bezerroplaca lucernifera*, Ecuador. **B.** *B. lucernifera*, Costa Rica. **C.** *B. fusconitida*, Costa Rica. **D.** *B. incrustatociliata*, Papua New Guinea, **E.** *B. pachyparaphysata*, Brazil. **F.** *B. streimannii*, Australia.

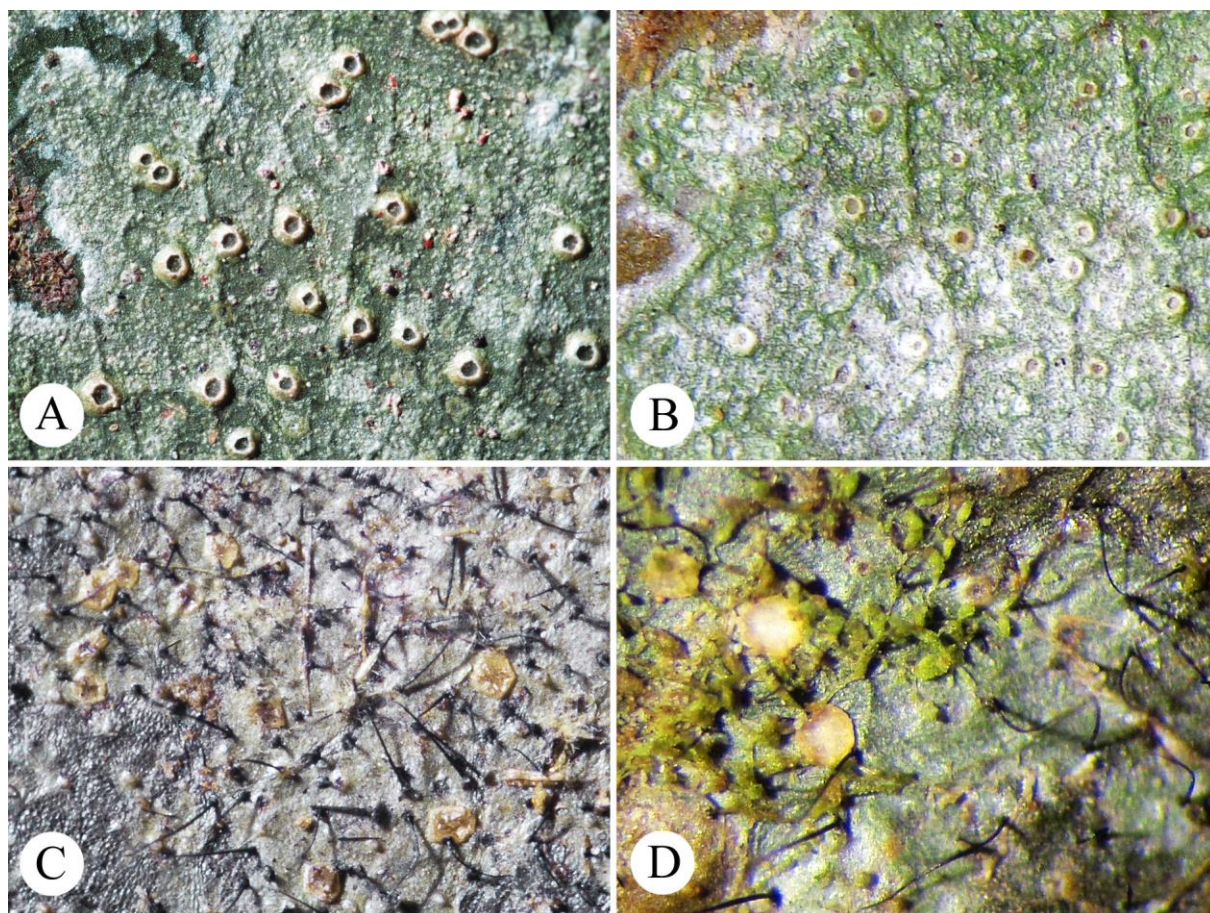


Figure 7: New genus *Caleniella* and reinstated genus *Microxyphiomyces*, including sequenced specimens. **A.** *Caleniella triseptata*, Costa Rica. **B.** *C. triseptata*, Brazil [23146]. **C.** *Microxyphiomyces lancicarpus*, French Guiana. **D.** *M. lancicarpus*, Brazil [22164].

Microxyphiomyces Bat., Valle & Peres

Mycobank MB 8944

Fig. 8 (A-F), Fig. 9 (A-D), Fig. 10 (A-D)

Microxyphiomyces Bat., Valle & Peres in Batista *et al.*, Publicações Inst. Micol. Recife 319: 8 (1961). Taxonomic synonym: *Setomyces* Bat. & Peres [nom. inval.] in Batista, Publicações, Instituto de Micologia da Universidade do Recife 320: 14 (1961).

Type species: *Microxyphiomyces manaosensis* Bat., Valle & Peres. = *Microxyphiomyces vainioi* (R. Sant.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.* [Mycobank MB 000000].

Basionym: *Tricharia vainioi* R. Sant., Symb. Bot. Upsal. 12(1): 382 (1952).

Diagnosis: Lichenized; thallus continuous, smooth, with black setae; apothecia sessile, biatorine, rarely erumpent and chroodiscoid; ascospores transversely septate to muriform;

hyphophores setiform, sometimes branched or hooked, black; diaphyphae filiform to moniliform.

Discussion: This genus is here resurrected to accommodate the *Tricharia vainioi* clade, which was already suspected to be distinct from *Tricharia* s.str. (Lücking *et al.* 2005) and in our molecular analysis appears only distantly related to the latter (Xavier-Leite *et al.* 2018a). The main diagnostic features are the smooth thallus and the more delicate setae, compared to the verrucose thallus and robust setae in *Tricharia* s.str. It should be noted that the genus as defined here includes three morphodemes: *Microxyphiomyces* s.str., with biatorine apothecia and unbranched hyphophores; the *T. lancicarpa* aggregate with chroodiscoid apothecia; and the *T. elegans* group with unique, branched-hooked hyphophores (Sérusiaux 1984). The latter has not yet been sequenced, so its inclusion in *Microxyphiomyces* is provisional. *Tricharia lancicarpa* differs from *Microxyphiomyces* s.str. in a similar way as *Roselviria* from *Spinomyces*, and in our phylogenetic analysis forms a supported sister clade (on a longer branch) to the latter, so the molecular evidence would allow to recognize this as a separate genus. We refrain from doing so until more species of the *T. vainioi* group have been sequenced.

Additional species included (see Xavier-Leite *et al.* 2018b):

Microxyphiomyces cuneatus (L.I. Ferraro & Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia cuneata* L.I. Ferraro & Vězda, *Bonplandia* 6: 112 (1989).

Microxyphiomyces demoulinii (Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia demoulinii* Sérus., *Mycologia* 76: 109 (1984).

Microxyphiomyces elegans (Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia elegans* Sérus., *Mycologia* 76: 110 (1984).

Microxyphiomyces kashiwadani (G. Thor, Lücking & Tat. Matsumoto) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia kashiwadani* G. Thor, Lücking & Tat. Matsumoto, *Symb. Bot. Upsal.* 32(3): 62 (2000).

Microxyphiomyces lancicarpus (Kalb & Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia lancicarpa* Kalb & Vězda, *Biblioth. Lichenol.* 29: 67 (1988).

Microxyphiomyces santessonianus (Kalb & Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia santessoniana* Kalb & Vězda, *Biblioth. Lichenol.* 29: 70 (1988).

Microxyphiomyces santessonii (D. Hawks.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia santessonii* D. Hawksw., *Lichenologist* 5: 321 (1972).

Microxyphiomyces similis (Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia similis* Vězda, *Folia Geobot. Phytotax.* 14: 75 (1979).

Microxyphiomyces variratae (Lücking & Sipman) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia variratae* Lücking & Sipman in Lücking *et al.*, *Lichenologist* 37: 166 (2005).

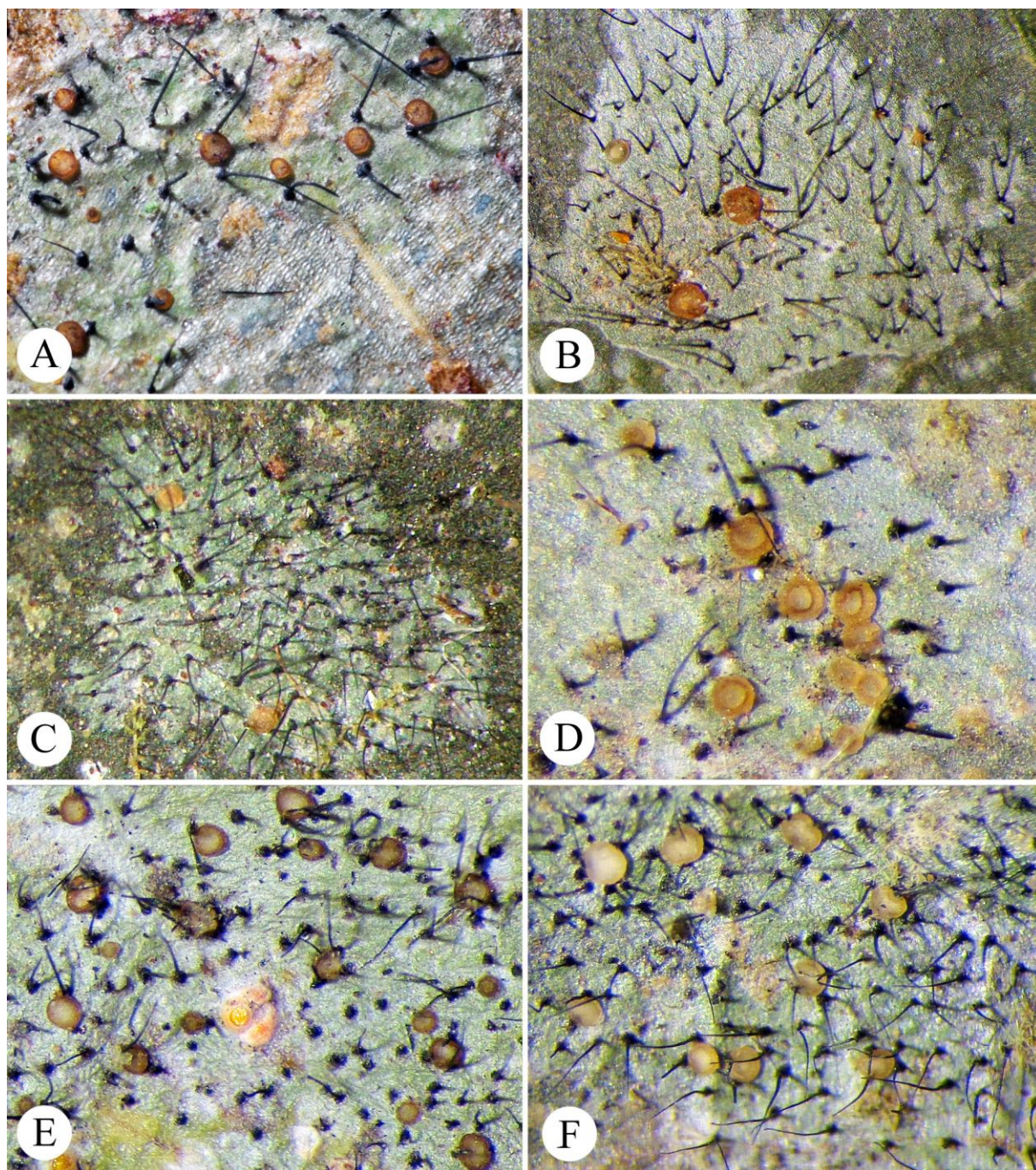


Figure 8: New genus *Microxyphiomyces*, including sequenced specimens. **A.** *Microxyphiomyces vainioi*, Costa Rica. **B.** *M. vainioi*, Brazil [22176]. **C.** *M. vainioi*, Brazil [22004]. **D.** *M. vainioi*, Brazil [23075]. **E.** *M. vainioi*, Brazil [23111]. **F.** *M. vainioi*, Brazil [23077].

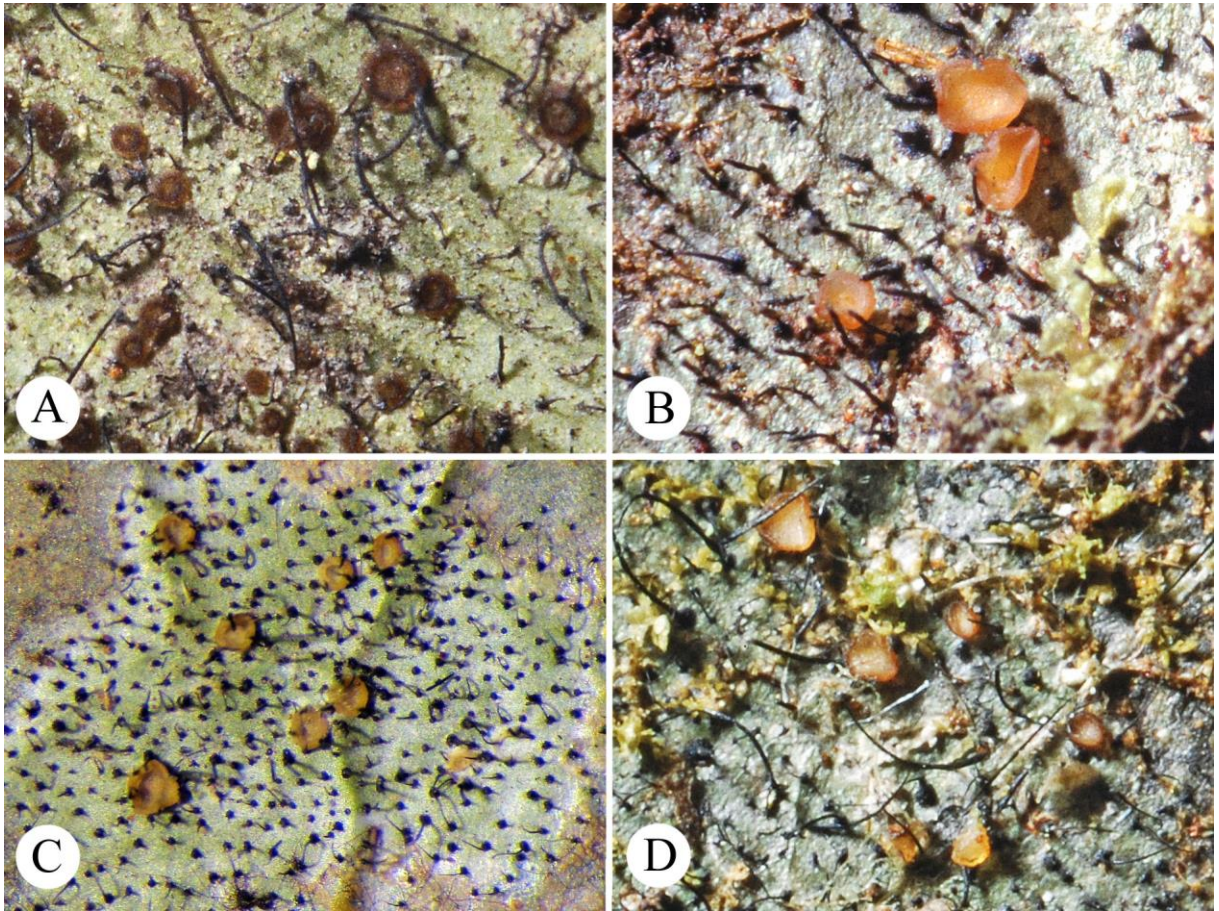


Figure 9: Reinstated genus *Microxyphiomyces*, including sequenced specimens. **A.** *Microxyphiomyces demoulinii*, Papua New Guinea. **B.** *M. similis*, holotype. **C.** *M. similis*, Brazil [22147]. **D.** *M. variratae*, holotype.

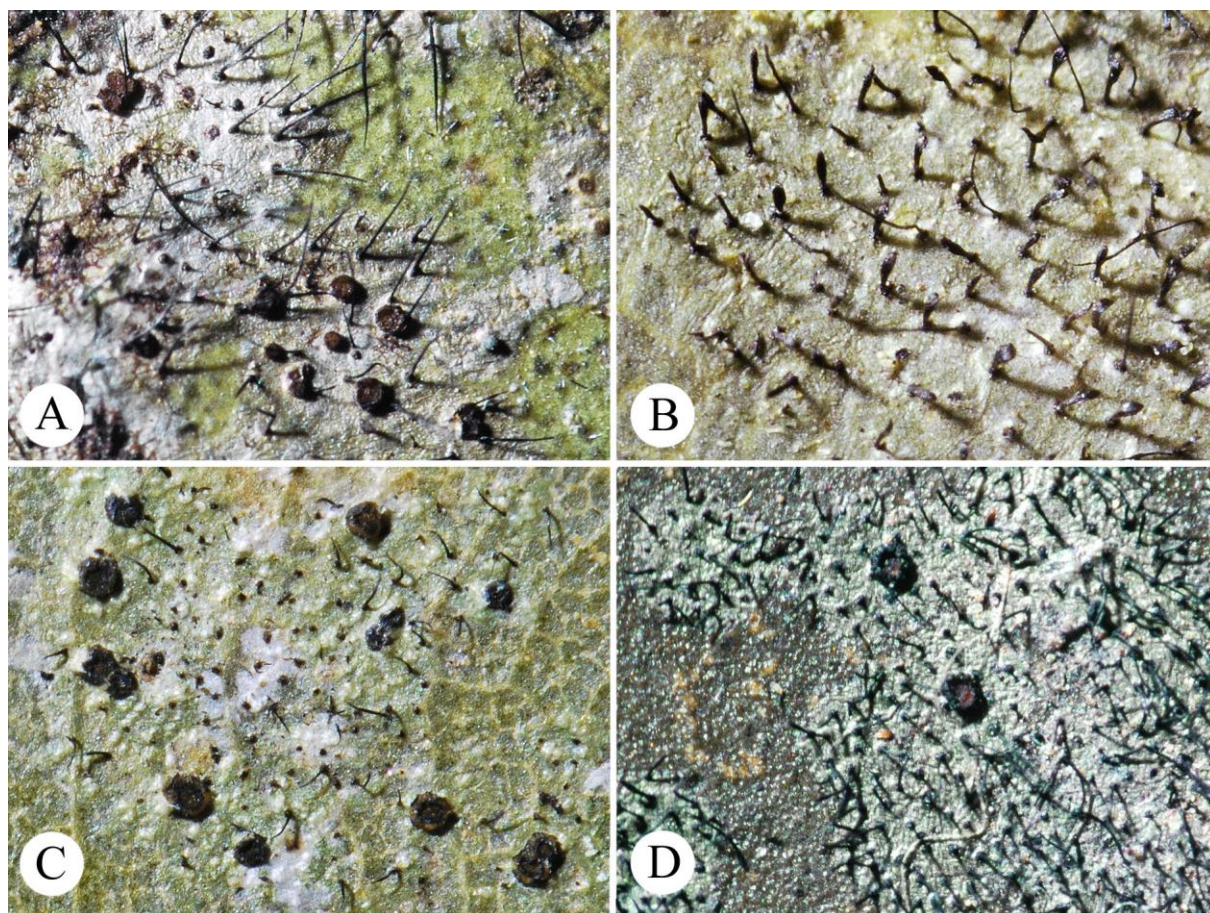


Figure 10: New genus *Microxyphiomyces*. **A.** *Microxyphiomyces cuneatus*, Paraguay. **B.** *M. cuneatus*, holotype. **C.** *M. kashiwadanii*, Japan. **D.** *M. santessoni*, holotype.

Monocalenia Xavier-Leite, M. Cáceres & Lüicking, *gen. nov.*

MycoBank MB 000000

Fig. 11 (A-B)

Type species: *Monocalenia monospora* (Vězda) Xavier-Leite, M. Cáceres & Lüicking, *comb. nov.* [MycoBank MB 000000]. Basionym: *Calenia monospora* Vězda, *Folia Geobot. Phytotax.* 14: 56 (1979).

Diagnosis: Lichenized; thallus continuous, smooth, lacking setae; apothecia erumpent, zeorine (*Calenia* type), with epithelial algae; ascospores single, muriform; hyphophores unknown.

Etymology: The generic name is a combination of *Calenia* with part of the epithet of the type species, referring to the single-spored asci.

Genus description: Thallus foliicolous, continuous, lacking setae. Apothecia erumpent, zeorine; disc pruinose; proper margin indistinct, thalline margin distinct, not prominent.

Excipulum prosoplectenchymatous, colorless. Hypothecium prosoplectenchymatous, colorless. Epithecium granular, with epithelial algae. Ascospores single, muriform. Hyphophores setiform, pale. Diahyphae inserted apically, moniliform, with fusiform segments.

Discussion: This new genus is established for a single species, *Calenia monospora*, which is unrelated to *Calenia* s.lat. and instead closely allied to *Asterothyrium* (Xavier-Leite *et al.* 2018a). The lineage is characterized by a unique combination of smooth thallus, calenioid apothecia with pruinose disc and epithelial algae, and short hyphophores with fusiform diahyphal segments. Most similar is *Calenia lueckingii*, which agrees in the presence of epithelial algae and in the muriform ascospores, but its thallus is finely verrucose and the apothecia lack pruina, thus being more similar to *Calenia* s.str. and molecular data suggest a close relationship of that species with the latter and not with *C. monospora* (Xavier-Leite *et al.* 2018a).

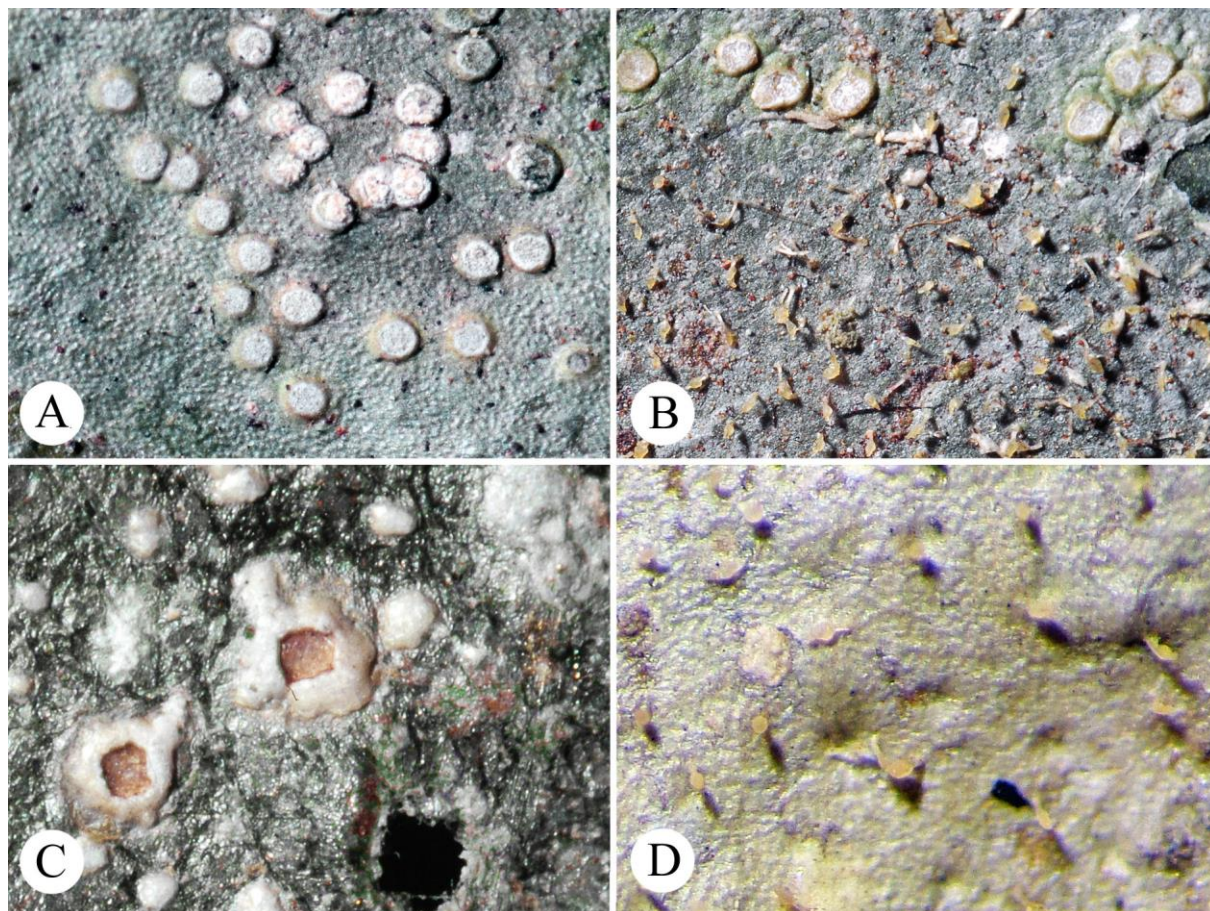


Figure 11: New genera *Monocalenia* and *Pseudocalenia*. **A.** *Monocalenia monospora*, Costa Rica. **B.** *M. monospora*, holotype. **C.** *Pseudocalenia solorinoides*, holotype. **D.** *Pseudocalenia* sp., Guatemala [22815].

Psathyromyces Bat. & Peres

Mycobank MB 9545

Fig. 12 (A-F)

Psathyromyces Bat. & Peres, Anais XIV Congr. Soc. Bot. Brasil: 95 (1964) [1963].

Type species: *Psathyromyces rosacearum* Bat. & Peres. = *Psathyromyces heterellus* (Stirt.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.* [Mycobank MB 000000]. Basionym: *Arthonia heterella* Stirt., Proc. Roy. Phil. Soc. Glasgow 11: 106 (1879) [1878]; *Echinoplaca heterella* (Stirt.) R. Sant., Symb. Bot. Upsal. 12(1): 372 (1952); *Tricharia heterella* (Stirt.) Lücking, Biblioth. Lichenol. 65: 82 (1997); *Aderkomyces heterellus* (Stirt.) Lücking, Sérus. & Vězda, Lichenologist 37: 162 (2005).

Diagnosis: Lichenized; thallus continuous, smooth, with white setae; apothecia applanate, biatorine, orange; ascospores small muriform; hyphophores setiform, long, white, with arrow-like, blackened apex; diaphyphae moniliform.

Discussion: This genus is resurrected to accommodate the *Aderkomyces heterellus* aggregate, which is unrelated to *Aderkomyces* s.str. (Xavier-Leite *et al.* 2018a) and differs from the latter in apothecial color and particularly in the very long, arrow-shaped hyphophores (Lücking *et al.* 2005). Apart from a second species included here, *A. planus*, the sequenced clade also indicates a further, yet undescribed species (Xavier-Leite *et al.* 2018a).

Additional species included (see Xavier-Leite *et al.* 2018b):

Psathyromyces planus (Vězda) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia plana* Vězda, Folia Geobot. Phytotax. 14: 74 (1979); *Aderkomyces planus* (Vězda) Lücking, Sérus. & Vězda, Lichenologist 37(2): 162 (2005).

Pseudocalenia Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*

MycoBank MB 000000

Fig. 11 (C-D)

Type species: *Pseudocalenia solorinoides* (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Calenia solorinoides* Lücking, Nova Hedwigia 52: 292 (1991).

Diagnosis: Lichenized; thallus dispersed, bullate, lacking setae; apothecia immersed in the bullate thallus patches; ascospores single, muriform; hyphophores shortly setiform, white with blackened apex: diahyphae with terminal segments fusiform to clavate.

Etymology: The generic name refers to the notion that this species was previously included in *Calenia* but is not related to that genus.

Genus description: Thallus foliicolous, dispersed, lacking setae. Apothecia immersed in bullate thallus patches, lacking a proper margin and the 'thalline' margin formed by the surrounding thallus. Excipulum prosoplectenchymatous, colorless. Hypothecium prosoplectenchymatous, colorless. Epithecium indistinct. Ascospores single, muriform. Hyphophores marginal on the thallus patches, shortly setiform, white but apically blackened. Diahyphae inserted apically, terminal segments fusiform to clavate.

Discussion: *Pseudocalenia* is another segregate from *Calenia* s.lat., based on the morphologically unique *C. solorinoides*, which is unrelated to *Calenia* s.lat. and appears more closely allied to the morphologically quite distinct genera *Roselviria* and *Serusiauxiella* (Xavier-Leite *et al.* 2018a). The immersed, emarginate apothecia resembling those of

Solorinella species may be the diagnostic apomorphy for this lineage; otherwise, the taxon is most similar to phylogenetically unrelated *C. bullatinoides* Lücking and *Bullatina aspidota* (Xavier-Leite *et al.* 2018a), suggesting that the underlying thallus morphology evolved several times independently in the family.

Roselviria Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*

MycoBank MB 000000

Fig. 13 (A-D)

Type species: *Roselviria purulhensis* (Lücking, Sérus. & Vězda) Xavier-Leite, Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia purulhensis* Lücking & Barillas in Lücking, *Biblioth. Lichenol.* 65: 88 (1997); *Aderkomyces purulhensis* (Lücking & Barillas) Lücking, Sérus. & Vězda, *Lichenologist* 37: 162 (2005).

Diagnosis: Lichenized; thallus continuous, smooth, with white setae; apothecia erumpent, zeorine with triangular thalline lobules (*Chroodiscus* type); ascospores muriform; hyphophores setiform, white; diaphyphae moniliform.

Etymology: Dedicated to our colleague and friend, Roselvira Barillas, a pioneer in the study of foliicolous lichens in Guatemala.

Genus description: Thallus foliicolous, continuous, with sterile, white setae. Apothecia erumpent, zeorine ('pseudozeorine'); disc pale; proper margin distinct, prominent, thalline margin distinct, forming triangular lobules formed by algal-free corticiform layer. Excipulum hyphal, colorless. Hypothecium prosoplectenchymatous, colorless. Epithecium indistinct. Ascospores muriform. Hyphophores setiform, white. Diahyphae inserted apically, moniliform, segments ellipsoid to fusiform or to drop-shaped.

Discussion: This new genus appears unrelated to *Aderkomyces* s.str. in our molecular analysis (Xavier-Leite *et al.* 2018a) and differs from typical members of that genus in the pale, chroodiscoid apothecia and the short, setiform hyphophores. Lücking *et al.* (2005) did not consider apothecial morphology in this case to be of systematic importance, but our molecular data not only demonstrate the opposite but also that the main feature connecting *Roselviria* with *Aderkomyces* s.str., the sterile white setae, evolved multiple times within the family.

Additional species included (see Xavier-Leite *et al.* 2018b):

Roselviria lobulimarginata (Sipman & Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Aderkomyces lobulimarginatus* Sipman & Lücking, *Lichenologist* 37: 162 (2005).

Serusiauxiella Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*

MycoBank MB 000000

Fig. 14 (A-F)

Type species: *Serusiauxiella farinosa* (R. Sant.) Xavier-Leite, Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia farinosa* R. Sant, *Symb. Bot. Upsal.* 12(1): 387 (1952).

Diagnosis: Lichenized; thallus continuous, coarsely verrucose, with black setae and dark brown prothallus; apothecia adnate to sessile, lecideine, with dark brown pruina; ascospores muriform; hyphophores setiform, black; diaphyphae moniliform.

Etymology: We are pleased to dedicate this new genus to our esteemed colleague and friend, Emmanuel Sérusiaux, for his numerous contributions to the knowledge of foliicolous lichens and lichenology in general.

Genus description: Thallus foliicolous, continuous, coarsely verrucose, with numerous, sterile black setae; a dark brown prothallus usually present. Apothecia adnate to broadly sessile, lecideine; disc and proper margin covered by a thick, dark brown pruina. Excipulum prosoplectenchymatous, dark brown. Hypothecium prosoplectenchymatous, colorless. Epithecium dark brown, granulose. Ascospores single, muriform. Hyphophores setiform, black. Diahyphae inserted apically, moniliform, segments sausage-shaped.

Discussion: This so far monospecific genus includes a species previously placed in *Tricharia* s.str. (Santesson 1952; Lücking 1997, 2008 Lücking *et al.* 2005) but apparently unrelated to the latter and instead closely related to the genus *Rubrotricha*, with which it shares almost no apomorphy (Xavier-Leite *et al.* 2018a). The only consistent difference of the new genus from all species placed in *Tricharia* s.str. are the unique, lecideine apothecia with a thick, dark chocolate-brown pruina.

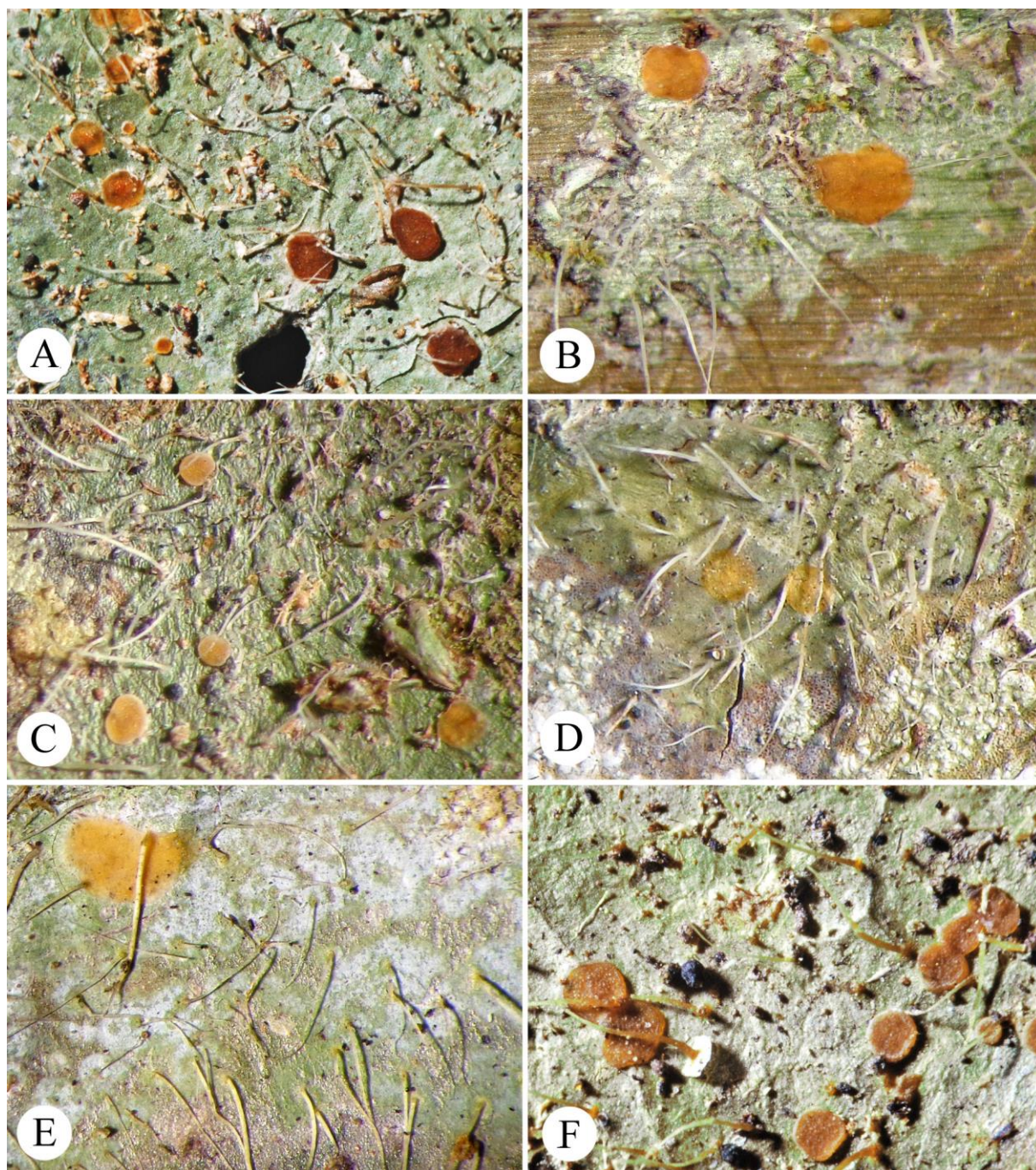


Figure 12: Reinstated genus *Psathyromyces*, including sequenced specimens. **A.** *Psathyromyces heterellus*, Guyana. **B.** *P. heterellus*, Brazil [22028]. **C.** *P. heterellus*, Brazil [22097]. **D.** *P. heterellus*, Brazil [22130]. **E.** *P. aff. heterellus*, Brazil [23163]. **F.** *P. planus* (Vězda) Xavier-Leite, M. Cáceres & Lücking, holotype.

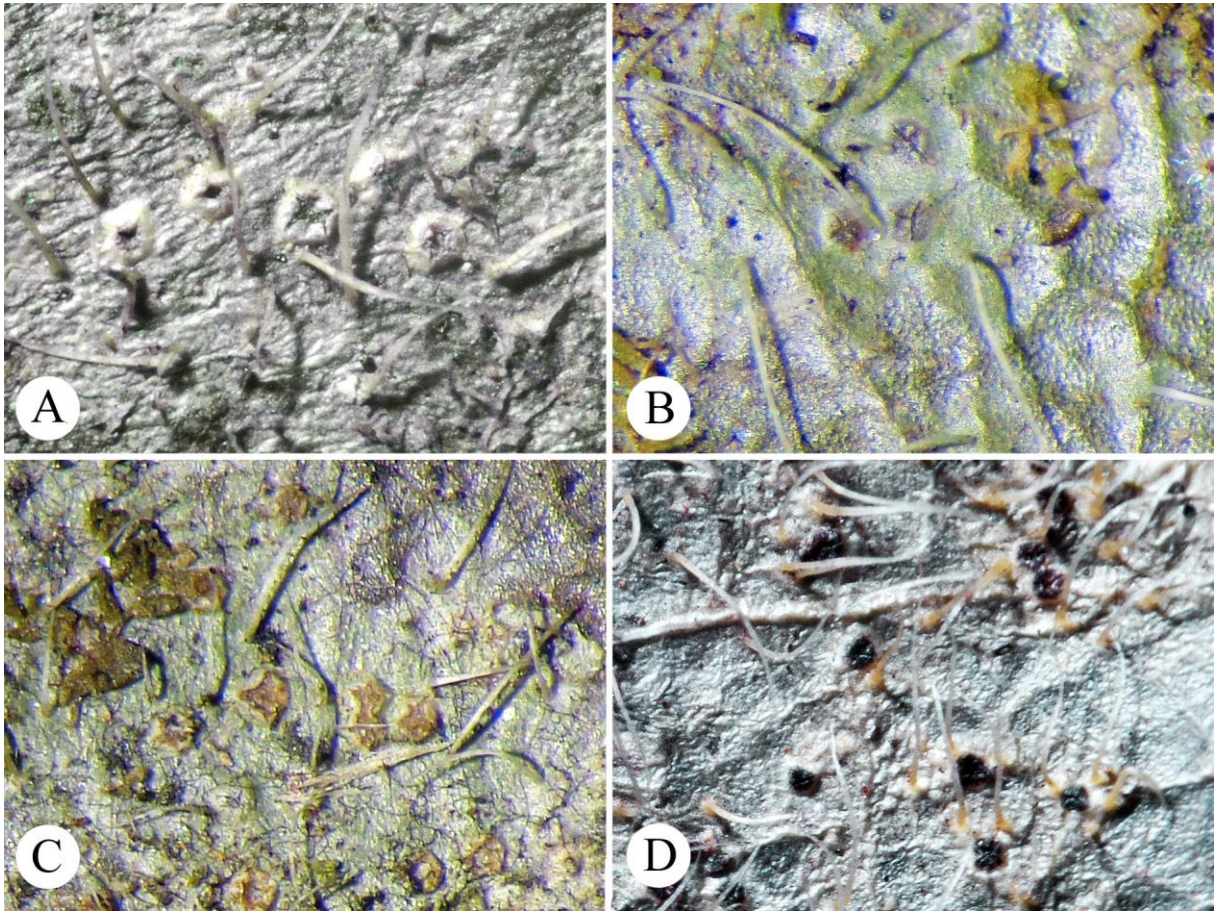


Figure 13: New genus *Roselviria*, including sequenced specimens. **A.** *Roselviria purulhensis*, Costa Rica. **B.** *R. purulhensis*, Brazil [22196]. **C.** *R. purulhensis*, Brazil [23104]. **D.** *R. lobulimarginata*, Malaysia (holotype).

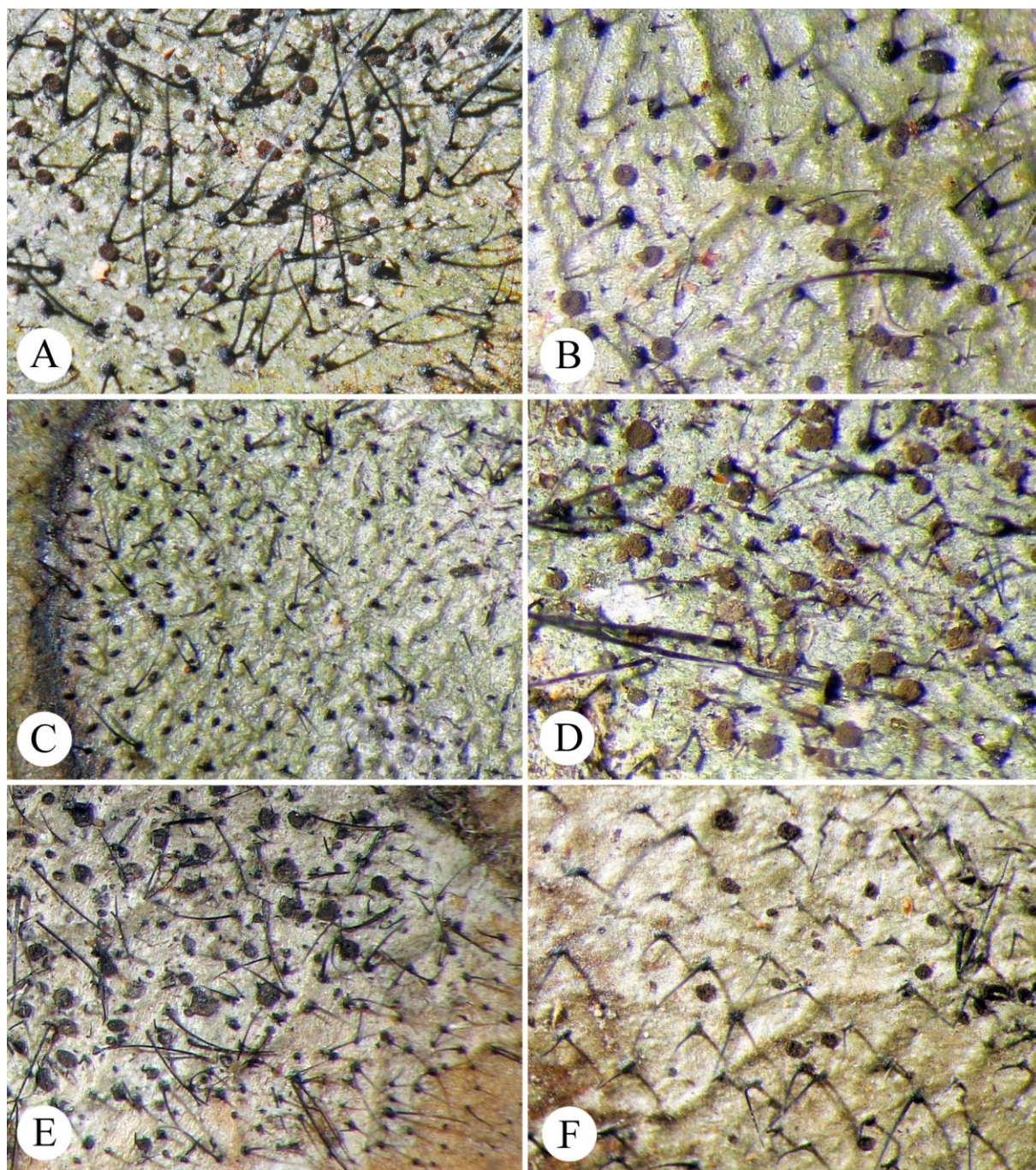


Figure 14: New genus *Serusiauxiella*, including sequenced specimens. **A** *Serusiauxiella farinosa*, Brazil. **B.** *S. farinosa*, Brazil [23062]. **C.** *S. farinosa*, Brazil [23063]. **D.** *S. farinosa*, Brazil [23065]. **E.** *S. aff. farinosa*, Guatemala [22801]. **F.** *S. aff. farinosa*, Guatemala [22809].

Sipmanidea Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*

MycoBank MB 000000

Fig. 15 (A-F)

Type species: *Sipmanidea neotropica* (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. et stat nov.* [MycoBank MB 000000]. Basionym: *Echinoplaca furcata* subsp. *neotropica* Lücking, Fl. Neotrop. Monogr. 103: 493 (2008).

Diagnosis: Lichenized; thallus continuous to dispersed, coarsely verrucose, usually whitish pruinose, with white, thinly branched setae usually formed on a translucent prothallus; apothecia erumpent to adnate, appearing zeorine to emarginate (*Calenia* or *Echinoplaca* type), orange; ascospores muriform; hyphophores setiform, yellowish; diaphyphae filiform with spermatozoid terminal segments.

Etymology: We dedicate this new genus to our esteemed colleague and friend, Harrie Sipman, one of the foremost tropical lichenologists who has also worked on foliicolous lichens.

Genus description: Thallus foliicolous, continuous to dispersed, coarsely verrucose, often whitish pruinose, with numerous, sterile white setae with short, lateral branches, usually formed on translucent prothallus. Apothecia erumpent and zeorine (calenioid) to adnate and spot-like (echinoplacoid); disc orange but usually with white, marginal pruina produced by needle-shaped crystals. Excipulum hyphal, colorless. Hypothecium prosoplectenchymatous, colorless. Epithecium yellowish brown, granular. Ascospores single, muriform. Hyphophores usually formed on the algiferous thallus, setiform, pale yellow. Diahyphae inserted subapically, composed of two types of filiform hyphae, either thick or thin, with the terminal segments of the thin hyphae strongly clavate to spermatozoid.

Discussion: This new genus corresponds to part of a group of species previously placed in *Echinoplaca* and considered unique due to their branched setae, unique thallus and apothecial pruina, and unique diahyphae (Lücking 1997; Lücking *et al.* 2005). In our molecular phylogenetic analysis, the species previously assigned to this group (*E. furcata* including subspecies, *E. verrucifera* including forms) formed two distinct, somehow related but separate clades, differing in apothecial morphology (at least in the sequenced species) and ascospore size and number per ascus). The sequenced taxon here assigned to the genus *Sipmanidea*, *E. furcata* subsp. *neotropica*, differs from the nominal subspecies in the distinctly calenioid apothecia; *E. furcata* subsp. *furcata* Sérus. has more echinoplacoid apothecia with an only slightly raised thalline margin..

Additional species included (see Xavier-Leite *et al.* 2018b):

Sipmanidea furcata (Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.* [MycoBank MB 000000]. Basionym: *Echinoplaca furcata* Sérus., Mycotaxon 35: 238 (1989).

Spinomyces Bat. & Peres ex Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*

MycoBank MB 000000

Fig. 16 (A-F)

Type species: *Spinomyces albostrigosus* (Lücking, Sérus. & Vězda) Xavier-Leite, Cáceres & Lücking, *comb. nov.* [MycoBank MB 000000]. Basionym: *Tricharia albostrigosa* R. Sant., Symb. Bot. Upsal. 12(1): 388 (1952); *Aderkomyces albostrigosus* (R. Sant.) Lücking, Sérus. & Vězda, Lichenologist 37: 161 (2005).

Diagnosis: Lichenized; thallus continuous, smooth, with white setae; apothecia sessile, biatorine; ascospores usually muriform; hyphophores setiform, white, often widened apically; diaphyphae moniliform.

Etymology: The name validated here likely refers to the sterile setae formed by these species.

Genus description: Thallus foliicolous, continuous, with sterile, white setae. Apothecia sessile, biatorine; disc variously coloured but usually yellowish to red-brown. Excipulum hyphal, colorless. Hypothecium prosoplectenchymatous, colorless. Epithecium indistinct. Ascospores mostly single, muriform. Hyphophores setiform with usually widened apex, white. Diahyphae inserted apically, moniliform, segments fusiform.

Discussion: The name *Spinomyces* was established without a description (Batista 1961), with the original material of the invalid name *S. genipae* based on a mixture of sterile specimens of *Tricharia* cf. *albostrigosa* and *Echinoplaca* sp. Since no name was available for the newly recognized clade centered around *Aderkomyces albostrigosus*, we decided to reinstate and validate the name *Spinomyces* for this clade. The species referred to this new genus were previously assigned to *Aderkomyces* (Lücking *et al.* 2005), which turned out to be highly polyphyletic based on molecular data (Xavier-Leite *et al.* 2018a). *Aderkomyces* s.str. appears to differ consistently by the applanate to adnate, more or less emarginate, dark greyish brown apothecia.

Additional species included (see Xavier-Leite *et al.* 2018b):

Spinomyces aggregatus (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. et stat. nov.* [MycoBank MB 000000]. Basionym: *Aderkomyces albostrigosus* f. *aggregatus* Lücking, Fl. Neotrop. Monogr. 103: 457 (2008).

Spinomyces deslooveri (Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.* [MycoBank MB 000000]. Basionym: *Tricharia deslooveri* Sérus. in Aptroot *et al.*, Biblioth. Lichenol. 64:

200 (1997); *Aderkomyces deslooveri* (Sérus.) Lücking, Sérus. & Vězda, *Lichenologist* 37: 161 (2005).

Spinomyces guatemalensis (Lücking & Barillas) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia guatemalensis* Lücking & Barillas in Lücking, *Biblioth. Lichenol.* 65: 81 (1997); *Aderkomyces guatemalensis* (Lücking & Barillas) Lücking, Sérus. & Vězda, *Lichenologist* 37: 161 (2005).

Spinomyces microcarpus (Etayo & Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia microcarpa* Etayo & Lücking in Etayo, *Flora y Fauna del Parque Nacional de Coiba (Panamá), Inventario Preliminar (Madrid)*: 217 (1997); *Aderkomyces microcarpus* (Etayo & Lücking) Lücking, Sérus. & Vězda, *Lichenologist* 37: 162 (2005).

Spinomyces verrucosus (Sérus.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Tricharia verrucosa* Sérus. in Aptroot *et al.*, *Biblioth. Lichenol.* 64: 204 (1997); *Aderkomyces verrucosus* (Sérus.) Lücking, Sérus. & Vězda, *Lichenologist* 37: 163 (2005).

***Sporocybomyces* H. Maia**

MycoBank MB 10031

Fig. 17 (A-F)

Sporocybomyces H. Maia in Batista & Maia, *Atas Inst. Micol. Univ. Pernambuco* 5: 60 (1967).

Type species: *Sporocybomyces pulcher* H. Maia. = *Sporocybomyces leucotrichoides* (Vain.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Calenia leucotrichoides* Vain., *Ann. Acad. Sci. Fenn., Ser. A*, 15(6): 166 (1921); *Echinoplaca leucotrichoides* (Vain.) R. Sant. in Thorold, *J. Ecol.* 40: 129 (1952).

Diagnosis: Lichenized; thallus continuous, finely verrucose, usually lacking sterile setae; apothecia adnate, spot-like (*Echinoplaca* type); ascospores large, transversely septate to muriform; hyphophores shortly setiform, blunt, white with darkened apices; diaphyphae filiform with clavate to sausage-shaped, multiseptate terminal segments.

Discussion: *Sporocybomyces* is another reinstated genus based on Batista and his co-workers, here used to accommodate the phylogenetically distinct *Echinoplaca leucotrichoides* clade (Xavier-Leite *et al.* 2018a). While the apothecia in this group are echinoplacoid, the diahyphae are unique in featuring multiseptate terminal segments (Lücking *et al.* 2005).

Additional species included (see Xavier-Leite *et al.* 2018b):

Sporocybomyces leucomuralis (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Echinoplaca leucomuralis* Lücking, Fl. Neotrop. Monogr. 103: 485 (2008).

Sporocybomyces macgregorii (Vain.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Arthonia macgregorii* Vain., Ann. Acad. Sci. Fenn., Ser. A, 15(6): 313 (1921); *Echinoplaca macgregorii* (Vain.) Lücking, Sérus. & Vězda, Lichenologist 37: 164 (2005).

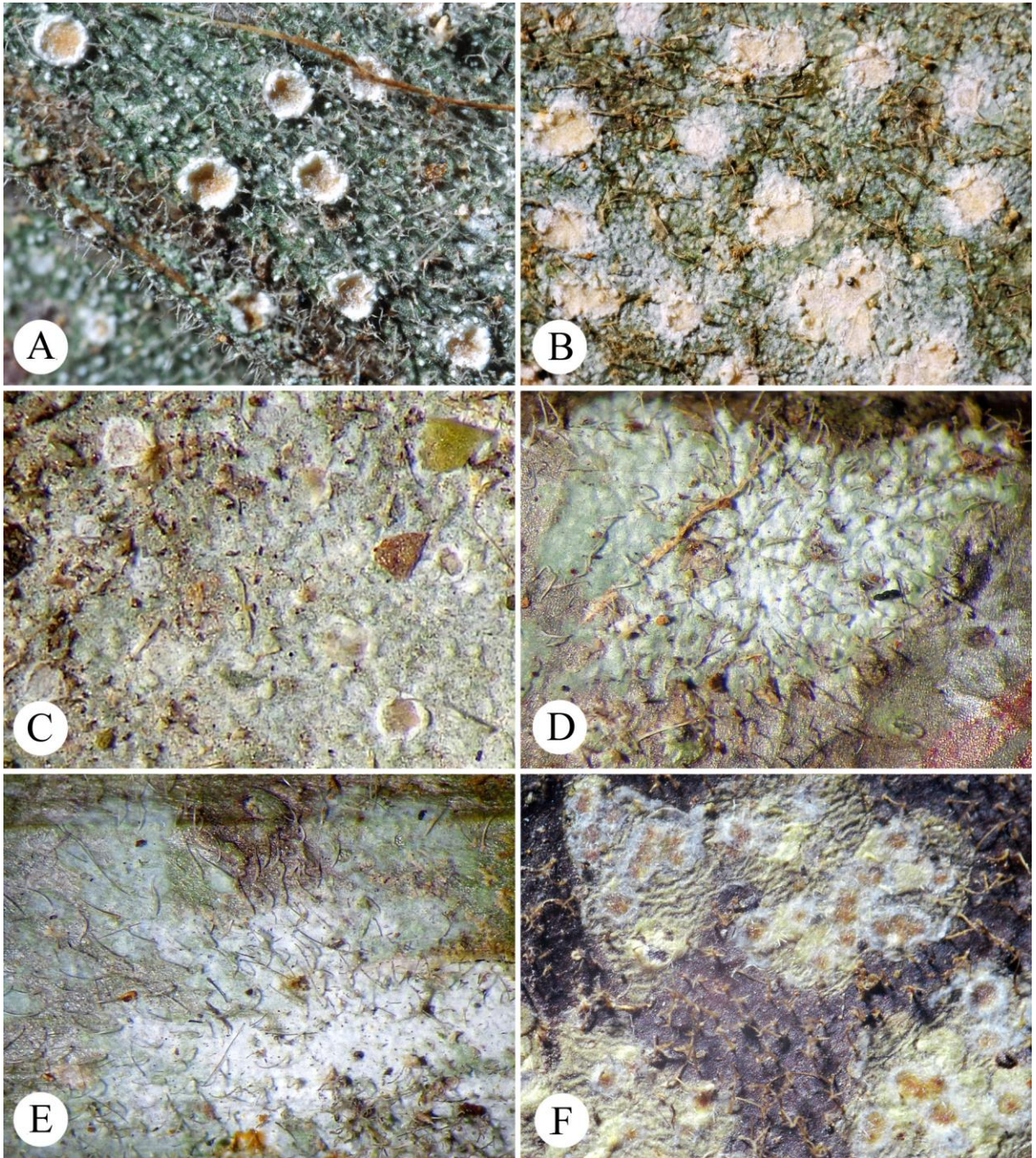


Figure 15: New genus *Sipmanidea*, including sequenced specimens. **A** *Sipmanidea neotropica*, Ecuador. **B.** *S. neotropica*, Ecuador. **C.** *S. neotropica*, Brazil [23016]. **D.** *S. neotropica*, Brazil [23143]. **E.** *S. neotropica*, Brazil [23144]. **F.** *S. furcata*, holotype.

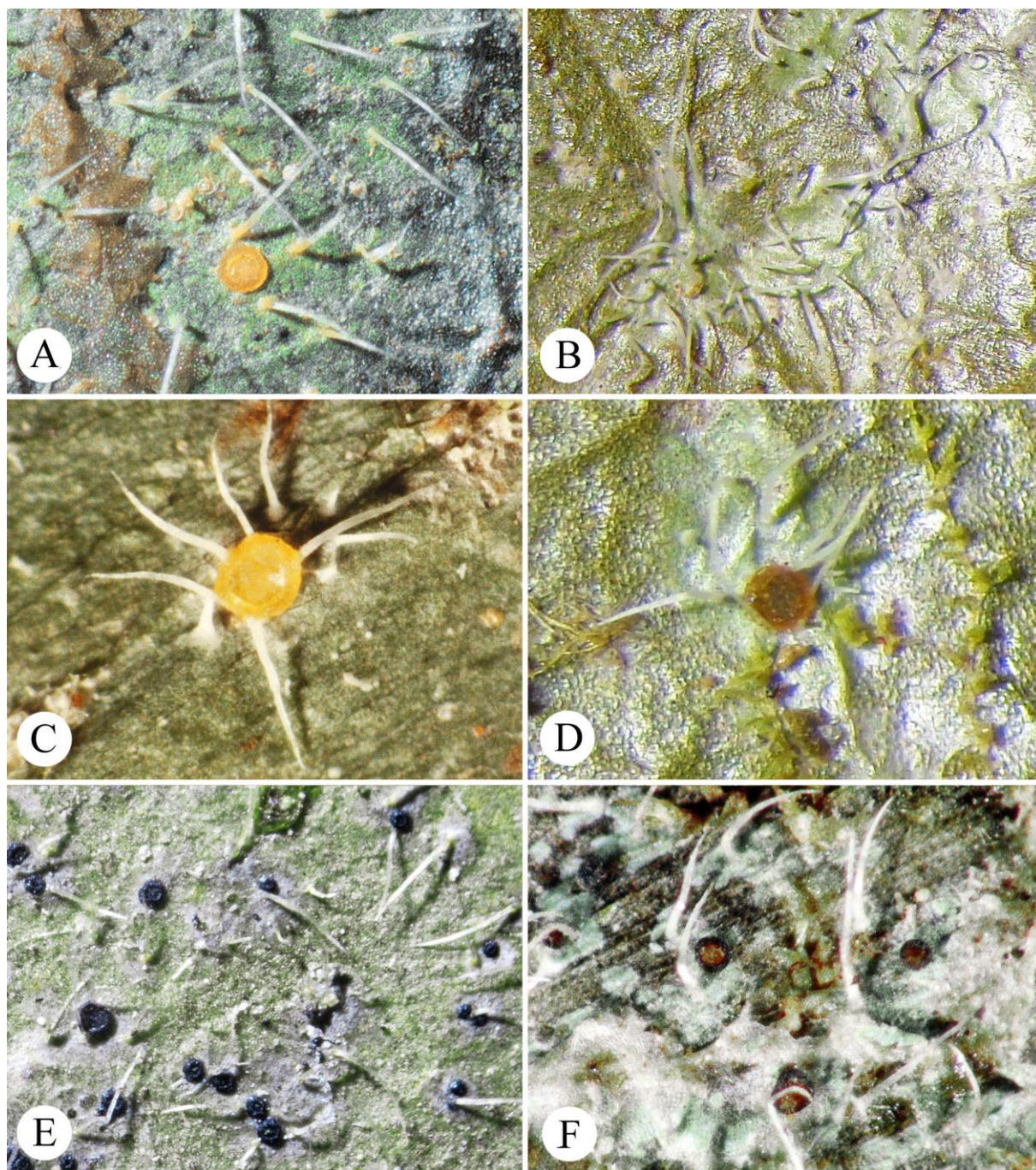


Figure 16: Reinstated and validated genus *Spinomyces*, including sequenced specimens. **A.** *Spinomyces albostrigosus*, Costa Rica. **B.** *S. albostrigosus*, Brazil [22194]. **C.** *S. aggregatus*, Guatemala. **D.** *S. aggregatus*, Brazil [22195]. **E.** *S. deslooveri*, holotype. **F.** *S. guatemalensis*, Guatemala.

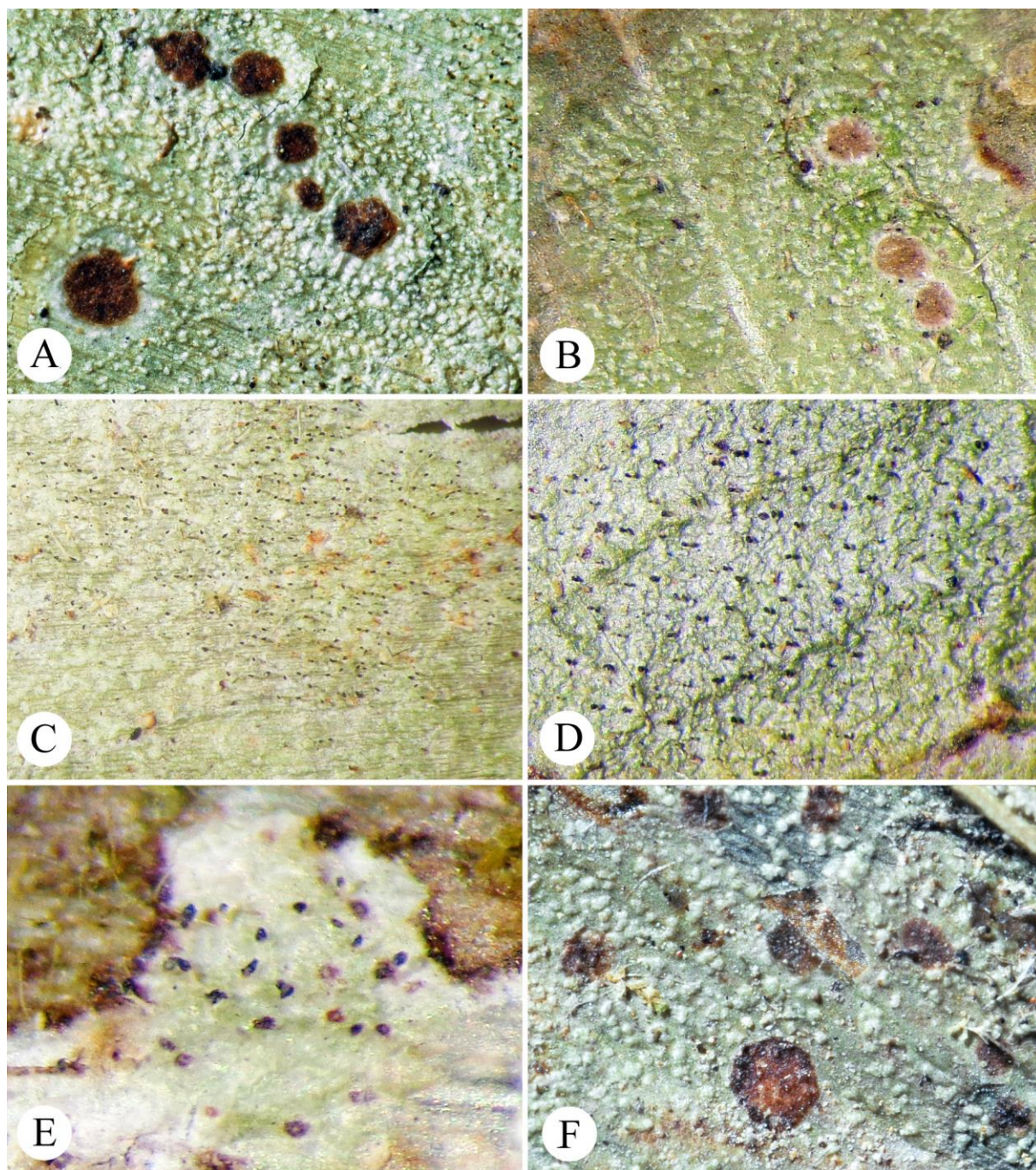


Figure 17: Reinstated genus *Sporocybomyces*, including sequenced specimens. **A** *Sporocybomyces leucotrichoides*, Costa Rica. **B.** *S. leucotrichoides*, Brazil [22046]. **C** *S. leucotrichoides*, Brazil [22030]. **D.** *S. leucotrichoides*, Brazil [23008]. **E.** *S. leucotrichoides*, Brazil [22013]. **F.** *S. leucomuralis*, Brazil.

Verruciplaca Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*

MycoBank MB 000000

Fig. 18 (A-F)

Type species: *Verruciplaca verrucifera* (Lücking) Xavier-Leite, Cáceres & Lücking, *comb. nov.*[MycoBank MB 000000]. Basionym: *Echinoplaca verrucifera* Lücking, *Biblioth. Lichenol.* 65: 62 (1997).

Diagnosis: Lichenized; thallus continuous to dispersed, coarsely verrucose, usually whitish to bluish pruinose, with white, thinly branched setae usually formed on a translucent prothallus; apothecia adnate, emarginate (*Echinoplaca* type), orange; ascospores small muriform; hyphophores setiform, yellowish; diahyphae filiform with spermatozoid terminal segments.

Etymology: The genus name refers to the large thallus verrucae typical of the new genus.

Genus description: Thallus foliicolous, continuous to dispersed, coarsely verrucose, usually whitish to bluish pruinose, with numerous, sterile white setae with short, lateral branches, usually formed on translucent prothallus. Apothecia adnate and spot-like (echinoplacoid); disc orange but often with white, marginal pruina produced by needle-shaped crystals. Excipulum hyphal, colorless. Hypothecium prosoplectenchymatous, colorless. Epithecium yellowish brown, granular. Ascospores usually 8 per ascus, muriform. Hyphophores formed on the algiferous thallus, setiform, pale yellow. Diahyphae inserted subapically, composed of two types of filiform hyphae, either thick or thin, with the terminal segments of the thin hyphae strongly clavate to spermatozoid.

Discussion: This new genus is similar to *Sipmanidea* in most aspects but forms a separate clade based on molecular evidence (see above). At present, ascospores are the main diagnostic feature, but sequence data for *Echinoplaca furcata* s.str. are needed to test this assumption. Lücking (2008) recognized only one species (with two forms) in the group forming the clade here named *Verruciplaca*, but our molecular data show that at least four distinct entities are involved (Xavier-Leite *et al.* 2018a). Two correspond to the two forms of *E. verrucifera* (f. *verrucifera* and f. *calcareae*), and therefore we elevate f. *calcareae* to species level here. The two as yet unnamed lineages will be formally described in a separate paper.

Additional species included (see Xavier-Leite *et al.* 2018b):

Verruciplaca calcarea (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. et stat. nov.* [MycoBank MB 000000]. Basionym: *Echinoplaca verrucifera* f. *calcareae* Lücking, *Fl. Neotrop. Monogr.* 103: 493 (2008).

Veždamyces Xavier-Leite, M. Cáceres & Lücking, *gen. nov.*

MycoBank MB 000000

Fig. 19 (A-F)

Type species: *Veždamyces vulgaris* (Müll. Arg.) Xavier-Leite, M. Cáceres & Lücking, *comb. nov.* [MycoBank MB 000000]. Basionym: *Lopadium vulgare* Müll. Arg., *Flora* 64: 109 (1881); *Tricharia vulgaris* (Müll. Arg.) R. Sant., *Symb. Bot. Upsal.* 12(1): 389 (1952); *Actinoplaca vulgaris* (Müll. Arg.) Vězda & Poelt, *Folia Geobot. Phytotax.* 22: 184 (1987); *Gyalideopsis vulgaris* (Müll. Arg.) Lücking, *Biblioth. Lichenol.* 65: 75 (1997).

Diagnosis: Lichenized; thallus continuous, finely verrucose, lacking sterile setae; apothecia adnate to sessile, biatorine; excipulum paraplectenchymatous; ascospores single, muriform; hyphophores shortly setiform, white with incrustation of crystals: diahyphae moniliform with clavate to spermatozoid segments.

Etymology: The genus name honours the legacy of Antonín Vězda, one of the prominent lichen taxonomists of the twentieth century who substantially advanced our knowledge of foliicolous lichen taxonomy and particularly of Gomphillaceae.

Genus description: Thallus foliicolous, continuous, finely verrucose, lacking sterile setae. Apothecia adnate to sessile, biatorine; disc greenish yellow, proper margin distinct, yellow or white pruinose. Excipulum paraplectenchymatous, colorless. Hypothecium prosoplectenchymatous, colorless. Epithecium with epithelial algae. Ascospores single, muriform. Hyphophores shortly setiform with thickened apex, pure white, encrusted with crystals. Diahyphae inserted apically, moniliform, segments clavate to spermatozoid, with scattered algal cells inbetween.

Discussion: The genus newly established here includes one of the most enigmatic species of Gomphillaceae, the systematic position of which has been a stumbling block prior to the results of our molecular phylogenetic analysis (Xavier-Leite *et al.* 2018b). Originally described in *Lopadium* due to the biatorine apothecia and muriform ascospores (Müller 1881), the genus was first transferred to *Tricharia* by Santesson (1952), who mistook the hyphophores for sterile setae but noticed their difference to the sterile setae found in other *Tricharia* species. Vězda & Poelt (1987) then included the species in *Actinoplaca*, mainly due to the presence of algae in the diahyphal bunches. Lücking (1997) challenged this placement, arguing that other than the diahyphal algae, the species differed from *Actinoplaca strigulacea*

in almost any possible way, including apothecial morphology and anatomy (echinoplacoid in *Actinoplaca* and lacking epithelial algae), ascospores (very small and 1-septate in *Actinoplaca*), and hyphophore and diahyphal type (sessile, globose diahyphal bunches with filiform diahyphae with only the terminal segments spermatozoid in *Actinoplaca*). The species was provisionally placed in *Gyalideopsis* based on apothecial morphology, but it was recognized that the paraplectenchymatous excipulum, epithelial algae, crystalline hyphophores and algiferous diaphyphal bunches strongly differed from all other species assigned to that genus (Lücking 1997, 2008; Lücking *et al.* 2005). Much to our surprise, while the molecular phylogeny supports the placement of this taxon in its genus, it is indeed closely related to *Actinoplaca strigulacea*, another example of the sometimes almost visionary systematic concept that characterized the work of Antonín Vězda. Our molecular data also support the distinction of the form with white-pruinose apothecial margins as a separate species and suggest the existence of a further, yet undescribed species from Brazil (Xavier-Leite *et al.* 2018b).

Additional species included (see Xavier-Leite *et al.* 2018b):

Vezdamyces albopruinosus (Lücking) Xavier-Leite, M. Cáceres & Lücking, *comb. et stat. nov.* [MycoBank MB 000000]. Basionym: *Gyalideopsis vulgaris* f. *albopruinosa* Lücking, Fl. Neotrop. Monogr. 103: 431 (2008).

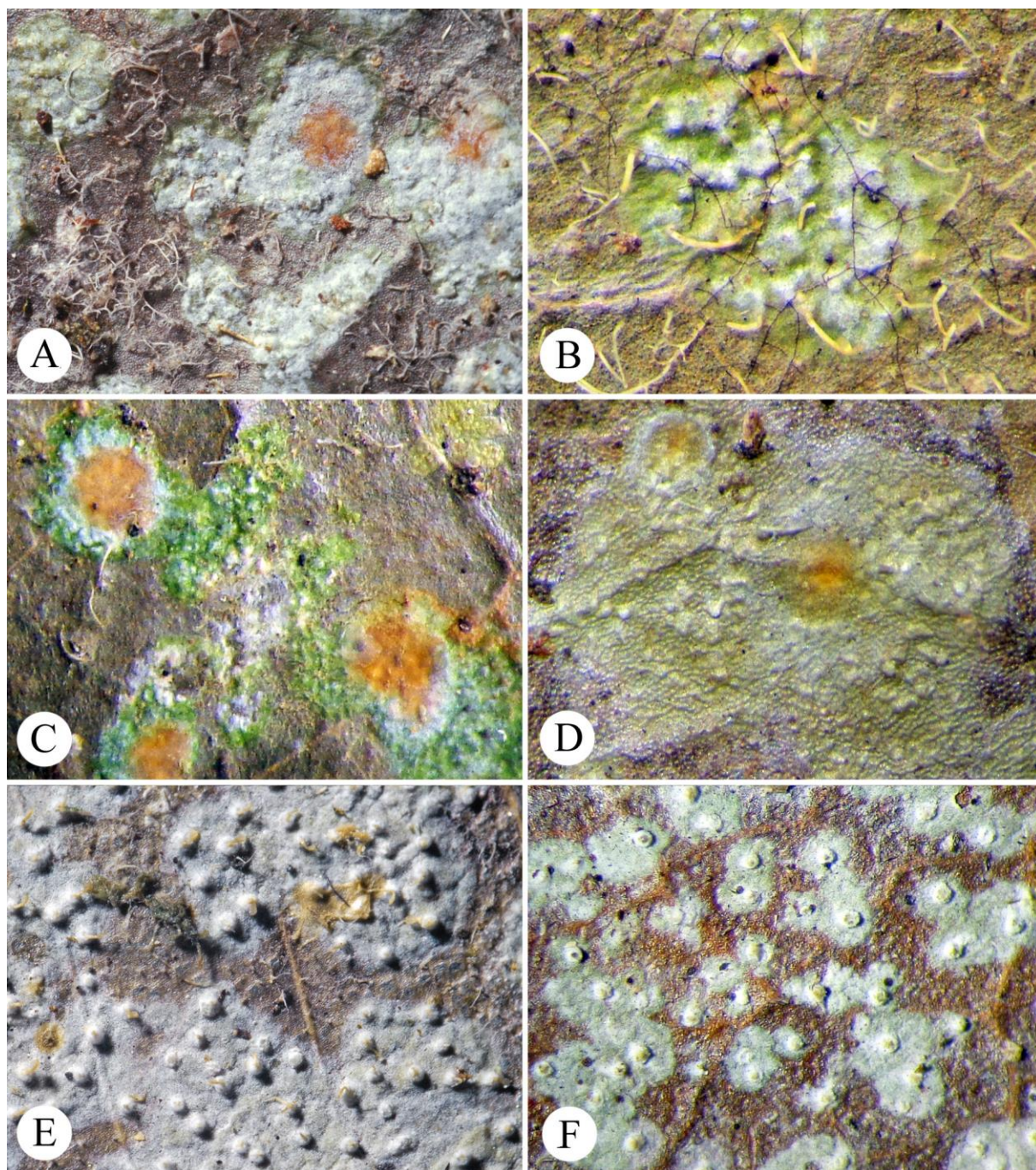


Figure 18: New genus *Verruciplaca*, including sequenced specimens. **A.** *Verruciplaca verrucifera*, Costa Rica. **B.** *V. verrucifera*, Brazil [22069]. **C.** *V. verrucifera*, Brazil [22068] **D.** *Verruciplaca* sp., Panama [22893]. **E.** *V. calcarea*, Costa Rica. **F.** *V. calcarea*, Brazil [22198].

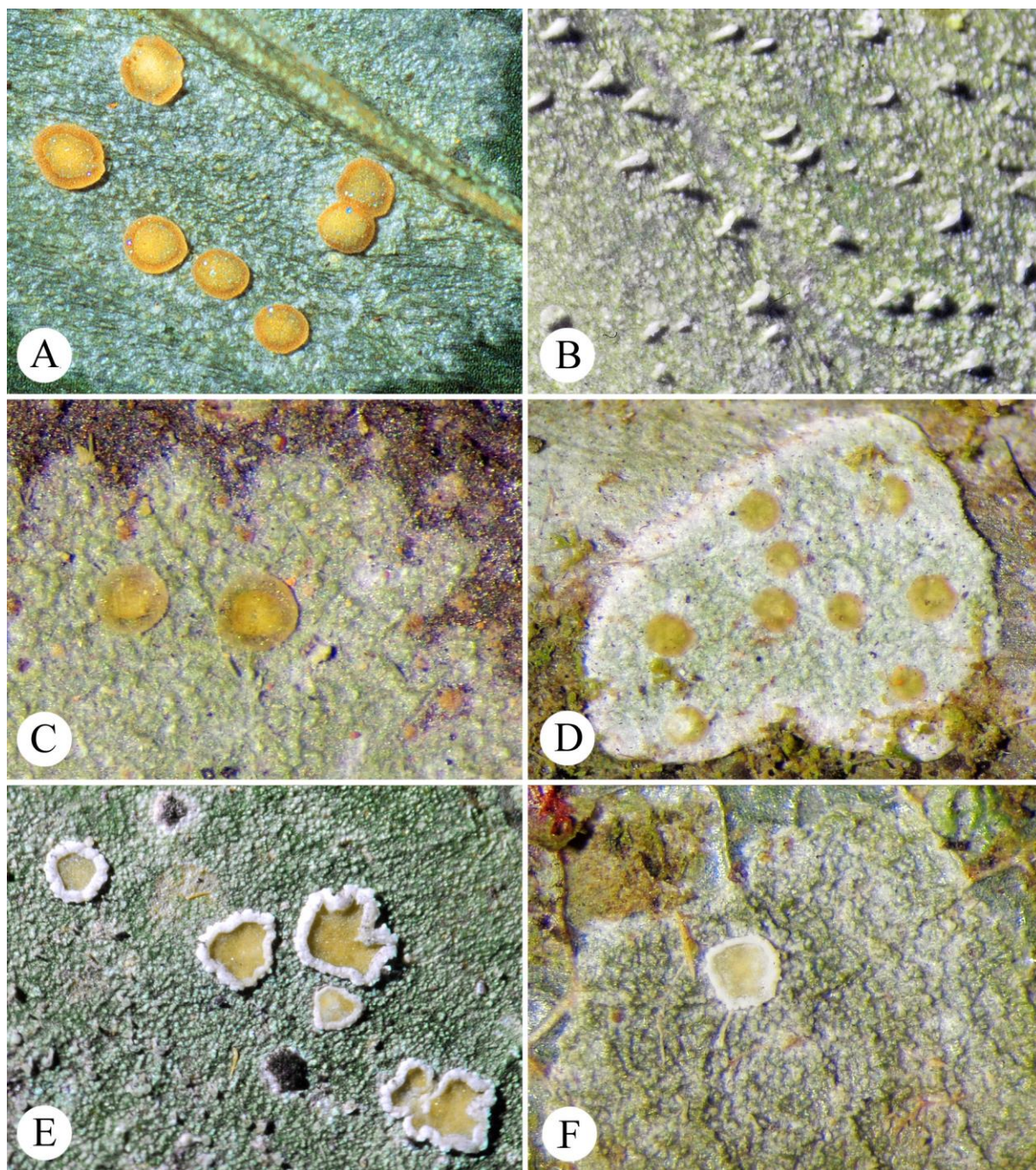


Figure 19: New genus *Vezdamyces*, including sequenced specimens. **A.** *Vezdamyces vulgaris*, Costa Rica. **B.** *V. vulgaris*, Costa Rica (hyphophores). **C.** *V. vulgaris*, Brazil [22145]. **D.** *V. aff. vulgaris*, Brazil [23047]. **E.** *V. albopruinosus*, Ecuador. **F.** *V. vulgaris*, Brazil [23052].

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 for 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).

4. REFERENCES

- Batista, A.C. 1961. Um pugilo de gêneros novos de líquens imperfeitos. *Publicações, Instituto de Micologia da Universidade de Recife* 320: 1–31.
- Batista, A.C., Peres, G.E.P. 1964. Líquens imperfeitos: novos gêneros e espécies de Manaus. *Anais do XIV Congresso da Sociedade Botânica do Brasil*: 89–102.
- Batista, A.C., Maia, H. da S. 1967. Novos líquens imperfeitos do Amazonas e de Pernambuco. *Atas do Instituto de Micologia da Universidade Federal de Pernambuco* 5: 55–71. (Publicações, Instituto de Micologia da Universidade do Recife 562).
- Batista, A.C., Poroca, D.J.M. 1970. Uma nova espécie de *Echinoplaca*, da Amazônia. *Publicações, Instituto de Micologia da Universidade Federal de Pernambuco* 635: 1–8.
- Duby, J. 1830. *Botanicon Gallicum* 2: 545-1068 +XLI-LVIII. Paris.
- Esslinger, T.L. 1975. A new north american species of the lichen genus *Gomphillus*. *Mycotaxon* 1: 189-192.
- Henssen, A. & Jahns, H.M. 1974. *Lichenes*. 467 pp. Stuttgart.
- Jahns, H.M. 1970. Untersuchungen zur Entwicklungsgeschichte der Cladoniaceen unter besonderer Berücksichtigung des Podetien-Problems. *Nova Hedwigia* 20: i–vi + 1–177.
- Lücking, R. 2008. Foliicolous lichenized fungi. *Flora Neotropica Monograph* 103: 1–873.
- Lücking, R., Sérusiaux, E., Maia, L.C., Pereira, E.C.G. 1998. A revision of the names of foliicolous lichenized fungi published by Batista and co-workers between 1960 and 1975. *The Lichenologist* 30: 121–191.
- Lücking, R., Stuart, B.L., 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.

- Lücking, R., Sérusiaux, E., Vězda, A. 2005. Phylogeny and systematics of the lichen family Gomphillaceae (Ostropales) inferred from cladistic analysis of phenotype data. *The Lichenologist* 37: 123–170.
- Lücking, R., Hodkinson, B.P., Leavitt, S.D. 2017 ('2016'). The 2016 classification of lichenized fungi in the Ascomycota and Basidiomycota – Approaching one thousand genera. *The Bryologist* 119: 361–416.
- Nylander, W. 1855. Essai d'une nouvelle classification des lichens (second memoire). *Mémoires de la Société des Sciences Naturelles* 3: 161–202.
- Nylander, W. 1860. De lichenibus nonnullis europaeis. *Flora* 43:545–54.
- Poelt, J. 1973. Classification. In: Ahmadjian, V. & Hale, M.E. (eds.). *The lichens*. Academic Press, New York and London, 599–632pp.
- Santesson, R. 1952. Foliicolous lichens I. A revision of the taxonomy of the obligately foliicolous, lichenized fungi. *Symbolae Botanicae Upsalienses* 12(1): 1–590.
- Vainio, E. 1896. Lichenes antillarum a W. R. Elliott collecti. *Journal of Botany* 34.
- Vězda, A. 1979. Flechtensystematische Studien. XI. Beiträge zur Kenntnis der Familie Asterothyriaceae (Discolichenes). *Folia Geobotanica Phytotaxonomica* 14: 43–94.
- Vězda, A. 1987. Flechtensystematische Studien. XII. Die Familie Gomphillaceae und ihre Gliederung. *Folia Geobotanica Phytotaxonomica* 22: 179–198.
- Xavier-Leite, A.B., Cáceres, M.E.S., Moncada, B., Lücking, R., Goto, B.T. 2018a. A phylogenetic revision of the classification of the lichenized family Gomphillaceae (Ascomycota: Ostropales), In prep.
- Xavier-Leite, A.B., Goto, B.T., Cáceres, M.E.S., Lücking, R. 2018b. Reclassification of species in the lichenized family Gomphillaceae (Ascomycota: Ostropales) using morphology-based phylogenetic binning, In prep.
- Zahlbruckner, A. 1905. Lichenes (Flechten) B. Spezieller Teil. Teil I, Abt. 1. In: Engler & Prantl, *Die Natürlichen Pflanzenfamilien*, 97–144pp.

Capítulo 3

Reclassification of species in the lichenized family Gomphillaceae (Ascomycota: Ostropales)
using morphology-based phylogenetic binning

Reclassification of species in the lichenized family Gomphillaceae (Ascomycota: Ostropales) using morphology-based phylogenetic binning

Amanda Barreto Xavier-Leite^{1,5}, Bruno Tomio Goto², Marcela E. da Silva Cáceres³ and Robert Lücking⁴

¹ *Programa de Pós-Graduação em Sistemática e Evolução, CB, Universidade Federal do Rio Grande do Norte, Campus Universitário, 59072-970, Natal, RN, Brazil;* ² *Departamento de Botânica e Zoologia, CB, Universidade Federal do Rio Grande do Norte, Campus Universitário, 59072-970, Natal, RN, Brazil;* ³ *Departamento de Biociências, Universidade Federal de Sergipe, CEP: 49500-000, Itabaiana, Sergipe, Brazil;* ⁴ *Botanischer Garten und Botanisches Museum, Freie Universität Berlin, Königin-Luise-Strasse 6–8, 14195 Berlin, Germany*

ABSTRACT

Results of phylogenetic analysis are often not translated into formal classifications, because only a portion of the taxa have been sequenced, thus making the placement of the remaining taxa unclear. This is also the case for Gomphillaceae, which currently includes 418 accepted species, with only little over 27% having sequence data available. A separate, updated phylogeny of the family recognized at least 17 new genus-level lineages, in addition to the 25 genera thus far distinguished, making it necessary to reassess generic placement of many additional species. In the present study we therefore applied the phylogenetic binning approach to this family. We selected a subset of 310 species, leaving out most species of *Gyalidea* and part of *Gyalideopsis* and *Gyalectidium*, because the phylogenetic framework was either too vague (*Gyalidea*, *Gyalideopsis*) or the genus was otherwise well-defined and clearly monophyletic (*Gyalectidium*). 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 node; another 24 taxa had between 70% and 89% support for a given node. Thus, 216 out of 238 taxa (91%) had 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

⁵ Corresponding author's e-mail: amandabxleite@hotmail.com

was in the reference tree; three further species of *Gyalideopsis* were placed with the outgroup. Most other taxa could be placed within a given genus with confidence, including the 17 newly recognized genera, and most placements obtained by phylogenetic binning were consistent with anticipated placements including from earlier studies, but for a small portion of the taxa (about 10%), the binning results were conflicting with their current or predicted placement. About 50 taxa were placed in one of the newly recognized genera based on our broader phylogenetic analysis and are formally recombined in a parallel paper.

Keywords. Foliicolous lichens, phenotype data, molecular data, phylogenetic binning, maximum likelihood

1. INTRODUCTION

Molecular phylogeny has revolutionized our understanding of relationships between taxa and their classification within the Fungi, all levels from domain down to species (Hibbett *et al.* 2007; McLaughlim *et al.* 2009; Berger *et al.* 2011b; Rivas-Plata *et al.* 2011b; Parmen *et al.* 2012; Rivas Plata *et al.* 2012a,b; Moncada *et al.* 2013; Lücking *et al.* 2015; Dal-Forno *et al.* 2016; Spatafora *et al.* 2016). In the Fungi, which have only a limited set of phenotype characters available, molecular data are of particular importance to correctly delimit and classify taxa (Hibbett *et al.* 2007; McLaughlim *et al.* 2009; Parmen *et al.* 2012; Rivas Plata *et al.* 2012). Traditionally, the classification of Fungi and other organisms has worked under the paradigm that taxa should be recognized through phenotypic characters. Molecular methods then provided a means to test this and re-investigate the phylogenetic relationships between lineages (Grube *et al.* 2004; Lücking *et al.* 2004; Lutzoni *et al.* 2004; James *et al.* 2006; Hibbett *et al.* 2007; Berger *et al.* 2011b; Parmen *et al.* 2012; Rivas Plata *et al.* 2012b; Lücking *et al.* 2015), so that the scientific community could adopt consensus classifications based on well-supported, monophyletic groups recommended for general use (Hibbett *et al.* 2007; Wijayawardene *et al.* 2018).

However, although sequencing methods have become relatively inexpensive and broadly available, generally only a fraction of all taxa in a group have molecular data available, usually because fresh material is needed and most species have restricted distributions and/or are rare. Therefore, results of phylogenetic analysis are often not translated into formal classifications, because only a portion of the taxa in question has been included in a study and the placement of the remaining taxa remains unclear. Examples are widespread among fungi and a prominent example of tropical lichen fungi is the

Graphidaceae, in which about 20% of the known species have been sequenced and in some genera, such as *Graphis*, only about 10% (Lücking 2009; Lücking *et al.* 2009; Berger *et al.* 2011b; Rivas-Plata *et al.* 2011a). Thus, with the profound changes in classification in this family (Berger *et al.* 2011b; Rivas Plata *et al.* 2012b; Parnmen *et al.* 2012a,b; Lücking *et al.* 2014; 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 provides a quantitative and testable means to place taxa based on phenotype data alone within a phylogenetic framework of taxa for which molecular data are available and phenotype data have been mapped (Berger *et al.* 2011a, b). This method was originally developed to place fossils into a phylogenetic tree to enable more precise calibrations, but can equally be applied to any analogous cases. Phylogenetic binning included 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 the included taxa and computing weights for each character based on its distribution over the tree (homoplastic and uninformative characters are downweighted); (3) invoking the Evolutionary Placement Algorithm (EPA) for all taxa lacking molecular data, which places ('bins') each taxon individually into the tree based on its phenotype characters and their weights derived from (2), including bootstrapping to evaluate consistency of the placement relative to subsets of the phenotype data (Berger *et al.* 2011a). The advantages of this method are that it is quantitative and provides a predictive, testable placement for each taxon and that it places each taxon individually into the tree, which means that large numbers of taxa can be processed rather quickly and computational time does not increase exponentially. 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 (Moncada *et al.* 2014).

Thus far, phylogenetic binning has been mostly used with lichen fungi, such as Graphidaceae, particularly the genera *Graphis* and *Allographa*, but also in tribe Ocellularieae and in the genera *Chapsa* s.lat. and *Leptotrema*, and Lobariaceae (Berger *et al.* 2011b; Rivas Plata *et al.* 2012b; Parnmen *et al.* 2012; Moncada *et al.* 2014; Lücking *et al.* 2015; Lücking & Kalb 2018). The method has also been employed for other groups of organisms, including plants and sponges (Koch *et al.* 2012; Fang *et al.* 2013; Dohrmann *et al.* 2017).

Here, we apply this approach to the lichenized family Gomphillaceae, which currently includes 418 accepted species (Lücking *et al.* 2017). Members of this family are mostly found

on leaves in wet tropical forests, but several lineages also occur on other substrata and extend into temperate regions (Lücking 1997; Lücking 2001; Lücking 2008). Up to the present, only 25 species (6%) had sequence data available, a proportion that was recently increased to 111 species (27%), including several putatively new taxa, by a much broader taxon sampling approach (Xavier-Leite *et al.* 2018b).

This study recognized at least 17 new genus-level lineages (Xavier-Leite *et al.* 2018b, c), in addition to the 25 genera thus far distinguished (Etayo 2017; Lücking *et al.* 2017), making it necessary to reassess generic placement of many additional species, particularly in the highly polyphyletic genera *Aderkomyces*, *Calenia*, *Echinoplaca*, *Gyalideopsis*, and *Tricharia*.

2. MATERIALS AND METHODS

2.1 Phenotype data

We built on the phenotype data matrix first assembled by Lücking *et al.* (2005). This matrix originally contained 209 characters tailored for Gomphillaceae, but it was here expanded to 223 characters to allow the inclusion of the taxa previously placed in Asterothyriaceae and Solorinellaceae, namely the genera *Asterothyrium*, *Gyalidea* (including *Solorinella*), *Linhartia*, *Phyllogyalidea*, and *Psorotheciopsis* (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 our phylogenetic analysis (Xavier-Leite *et al.* 2018b). In addition, some characters were accommodated to include the outgroup (Supplemental Material 2).

While in the phylogenetic analysis, we opted for *Fissurina* (Graphidaceae) as outgroup, as the most closely related clade, in the binning analysis we adopted *Coenogonium*, with is a proper outgroup for both Gomphillaceae and Graphidaceae and provides a better model for the evaluation of ancestral apothecial types in these taxa. The 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 pycnidial morphology and anatomy (10). The matrix contained a total of 310 ingroup taxa (Supplemental Material 3), about 75% of the accepted species, excluding most species of *Gyalidea* and about one third of *Gyalideopsis*, since the phylogenetic sampling for these taxa was insufficient to provide a reliable binning result. We also included only a part of

the genus *Gyalectidium*, since this genus was shown to be very distinct and monophyletic in all studies (Ferraro *et al.* 2001; Lücking *et al.* 2005; Xavier-Leite *et al.* 2018b).

2.2 Molecular reference tree

We first ran the same data set as Xavier-Leite *et al.* (2018b), based on two molecular markers, the mitochondrial small subunit (mtSSU) and the nuclear large subunit (nuLSU) rDNA, but with three *Coenogonium* species as outgroup. We then used a subset of the data, representing one terminal per confirmed species, including 72 ingroup species and three outgroup taxa. To compute the reference tree for the phylogenetic binning, the aligned dataset was again subjected to maximum likelihood (ML) tree search using RAxML 8.2.0 (Stamatakis 2006, 2014; Stamatakis *et al.* 2008) employing a universal GTR-gamma model with ten ML searches. However, to avoid topological effects of sampling bias compared to the complete data set, the topology was constrained under RAxML using the topology of the full data set.

2.3 Phylogenetic binning

With 75 taxa in the molecular reference tree and 313 in the full phenotype matrix, our approach 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 that reflected the distribution of the phenotypic character states over the reference tree. Subsequently, applying the weight vector, the 238 additional taxa were placed as query taxa on 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; 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". In addition, the resulting classification table was converted from text into table format to highlight the results for each taxon.

3. RESULTS

The molecular reference tree included 36 genus-level lineages, out of the 42 now recognized based on our previous phylogenetic study (Fig. 1). 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 (Supplemental Material 4; Table 1;

Figs. 2–5). Further 35 taxa appeared on two or more alternative nodes but had at least 90% support for one node; another 24 taxa had between 70% and 89% support for a given node. Thus, 216 out of 238 taxa (91%) had 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. The remaining species were binned into one of the 36 genera in the reference tree. For 22 species (9%), the placement was unresolved (Table 1; Figs. 2–5).

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. Most of these again represented the genus *Gyalideopsis*, the largest genus in the family with over 100 species but for which only few sequenced reference taxa were available. About 50 taxa were placed in one of the newly recognized genera based on our broader phylogenetic analysis (Xavier-Leite *et al.* 2018b) and are formally recombined in a parallel paper (Xavier-Leite *et al.* 2018c).

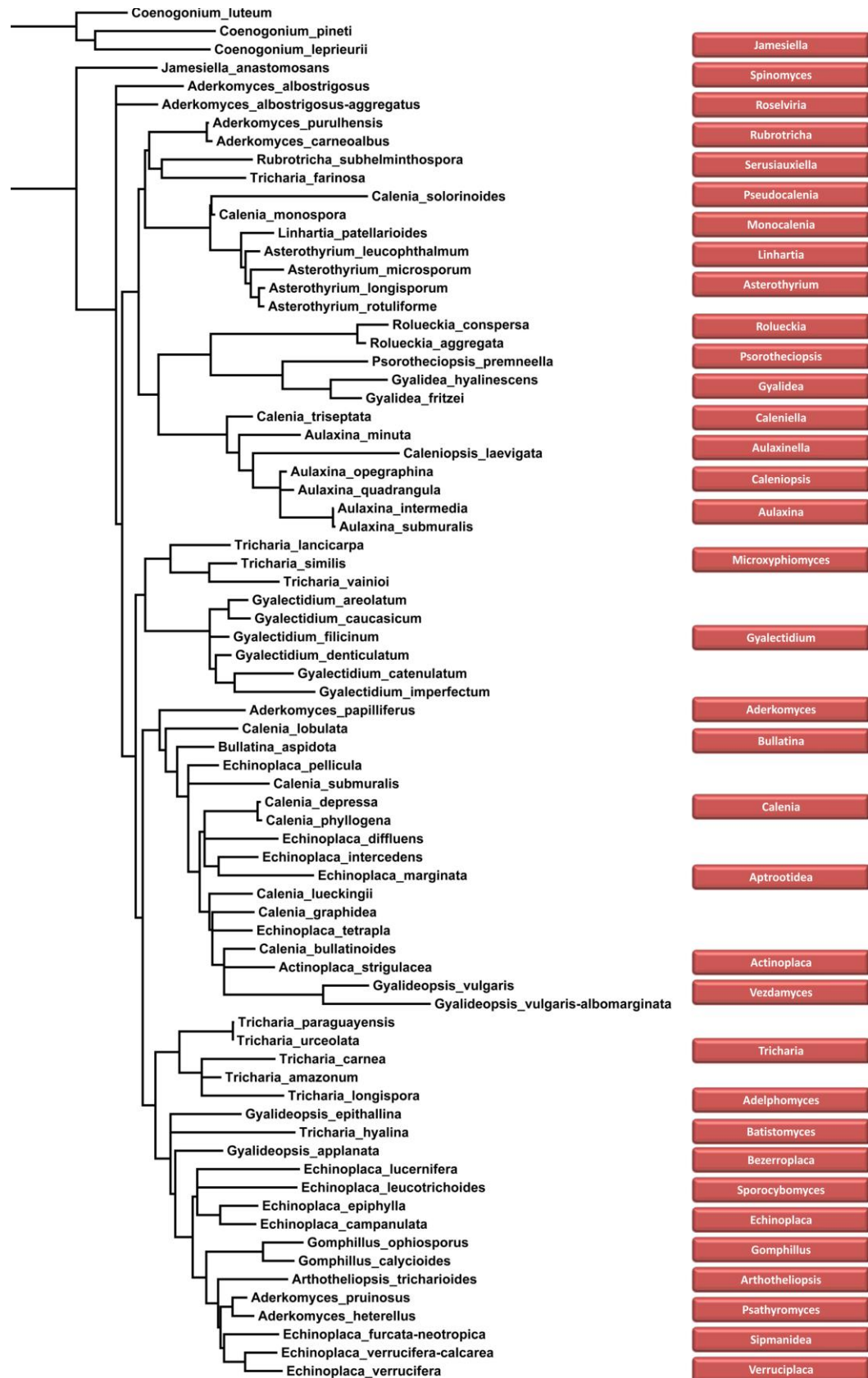


Figure 1: The molecular reference tree (maximum likelihood tree) showing 36 genus-level lineages of Gomphillaceae and the relationships among genera. The molecular phylogenetic analysis presented and confirmed 13 new genera and four newly reinstated genera for the family.

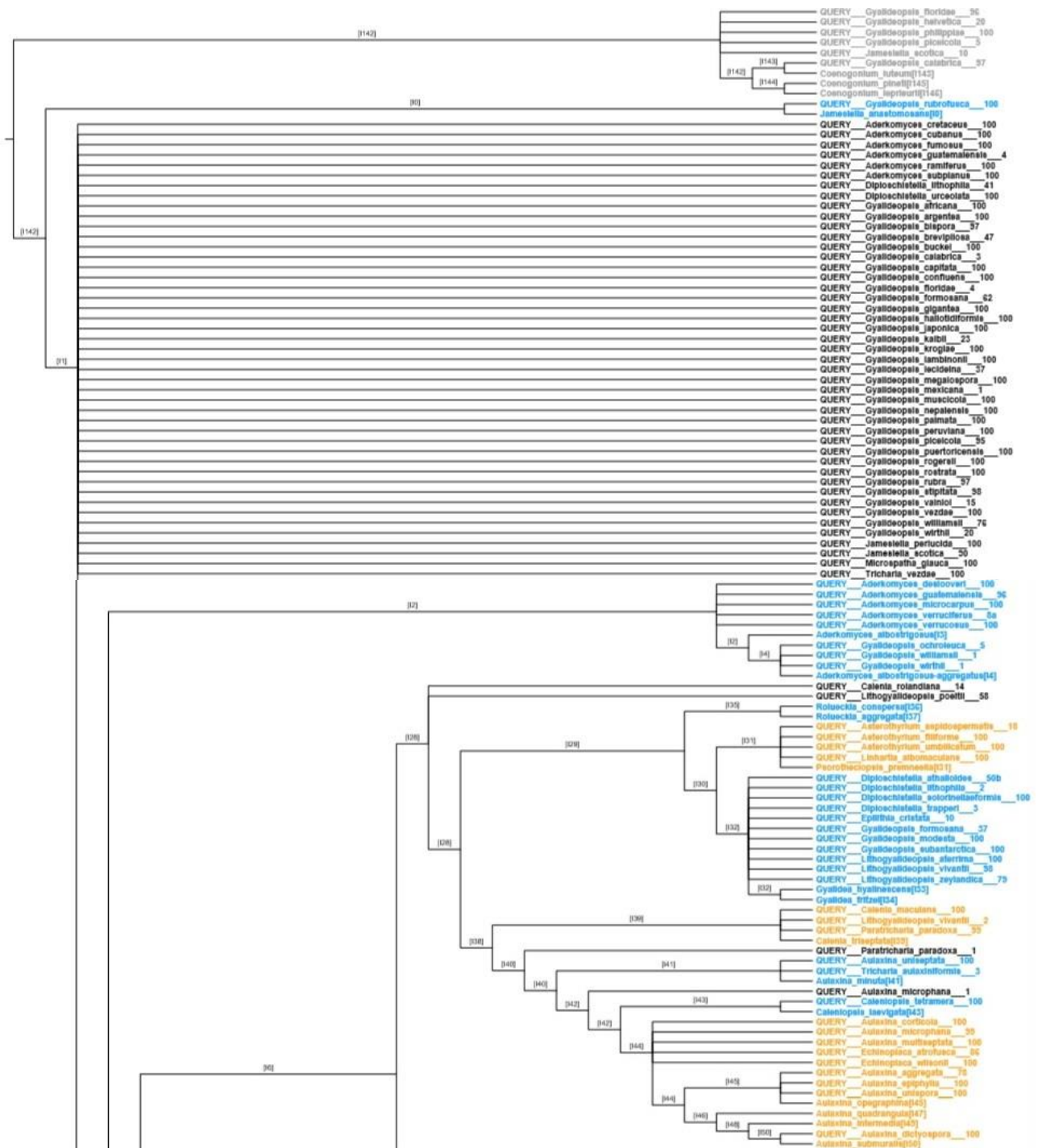


Figure 2–5: Result of the method of morphology-based phylogenetic binning using taxa in the molecular reference and taxa based on their phenotype characters. The analysis include node identifications (ID) number and bootstrap support numbers after the query name from the RAxML analysis.

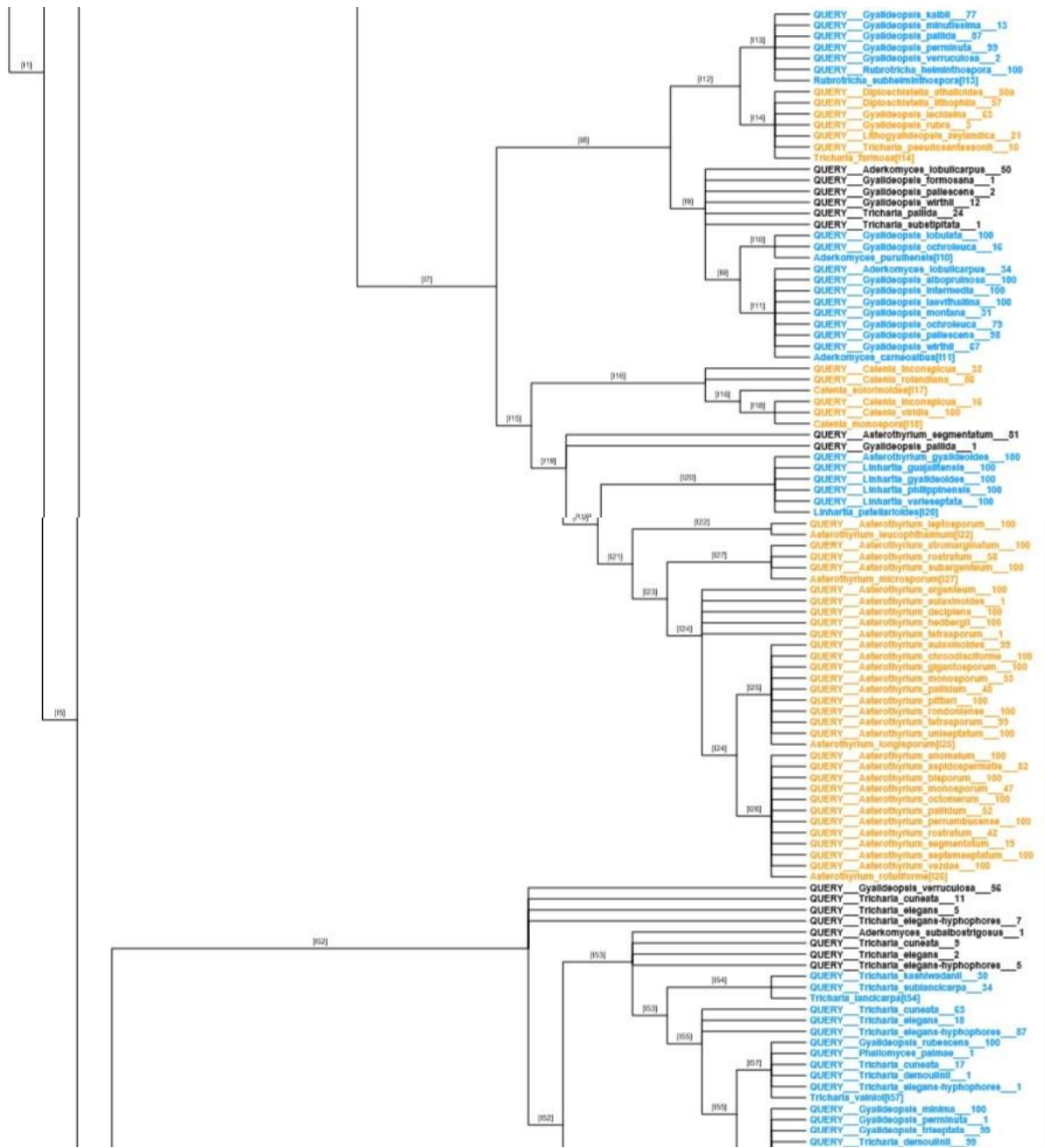


Figure 2–5: Result of the method of morphology-based phylogenetic binning using taxa in the molecular reference and taxa based on their phenotype characters. The analysis include node identifications (ID) number and bootstrap support numbers after the query name from the RAxML analysis.

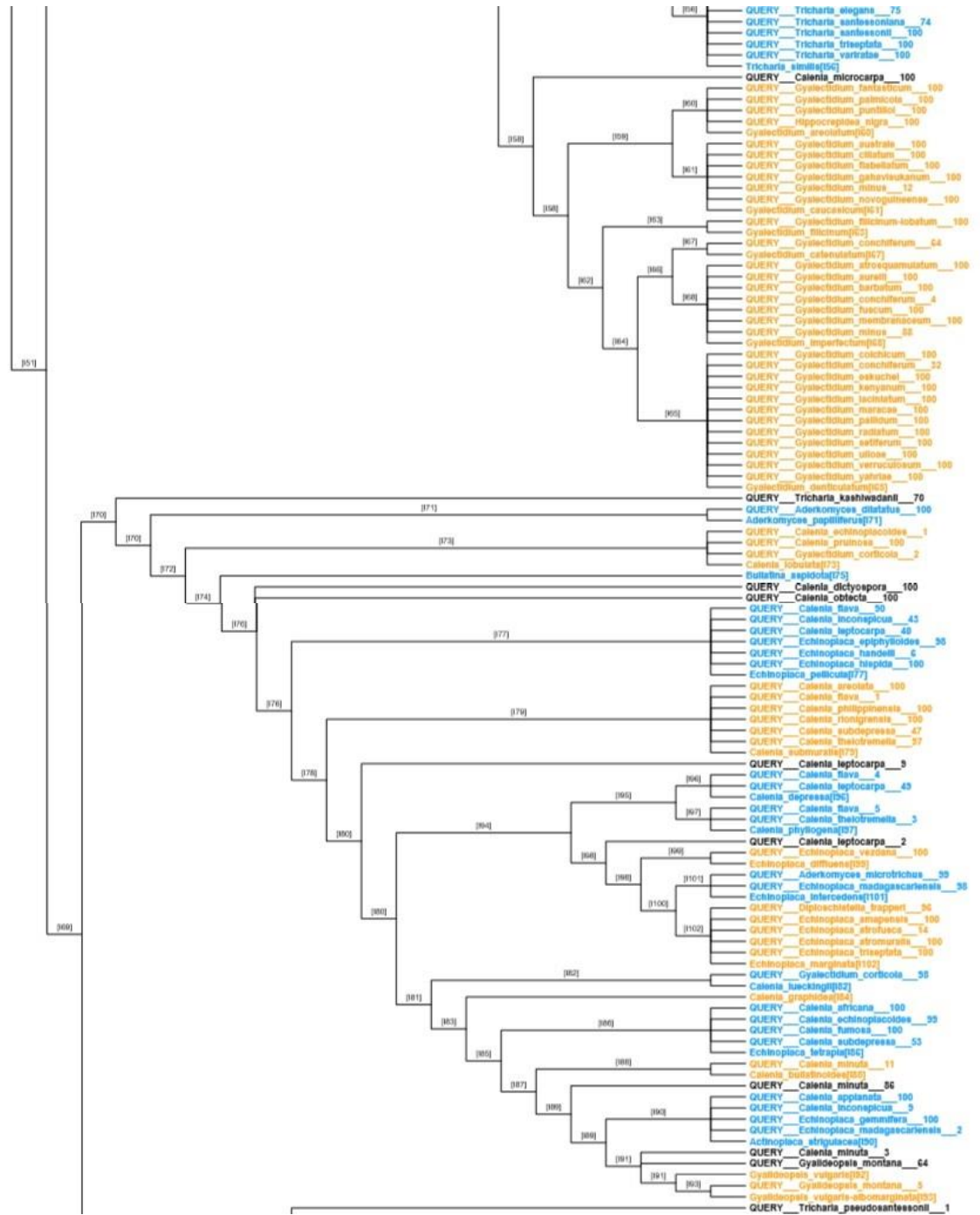


Figure 2–5: Result of the method of morphology-based phylogenetic binning using taxa in the molecular reference and taxa based on their phenotype characters. The analysis include node identifications (ID) numbers on each branch and bootstrap support values from RAXML after the query name.

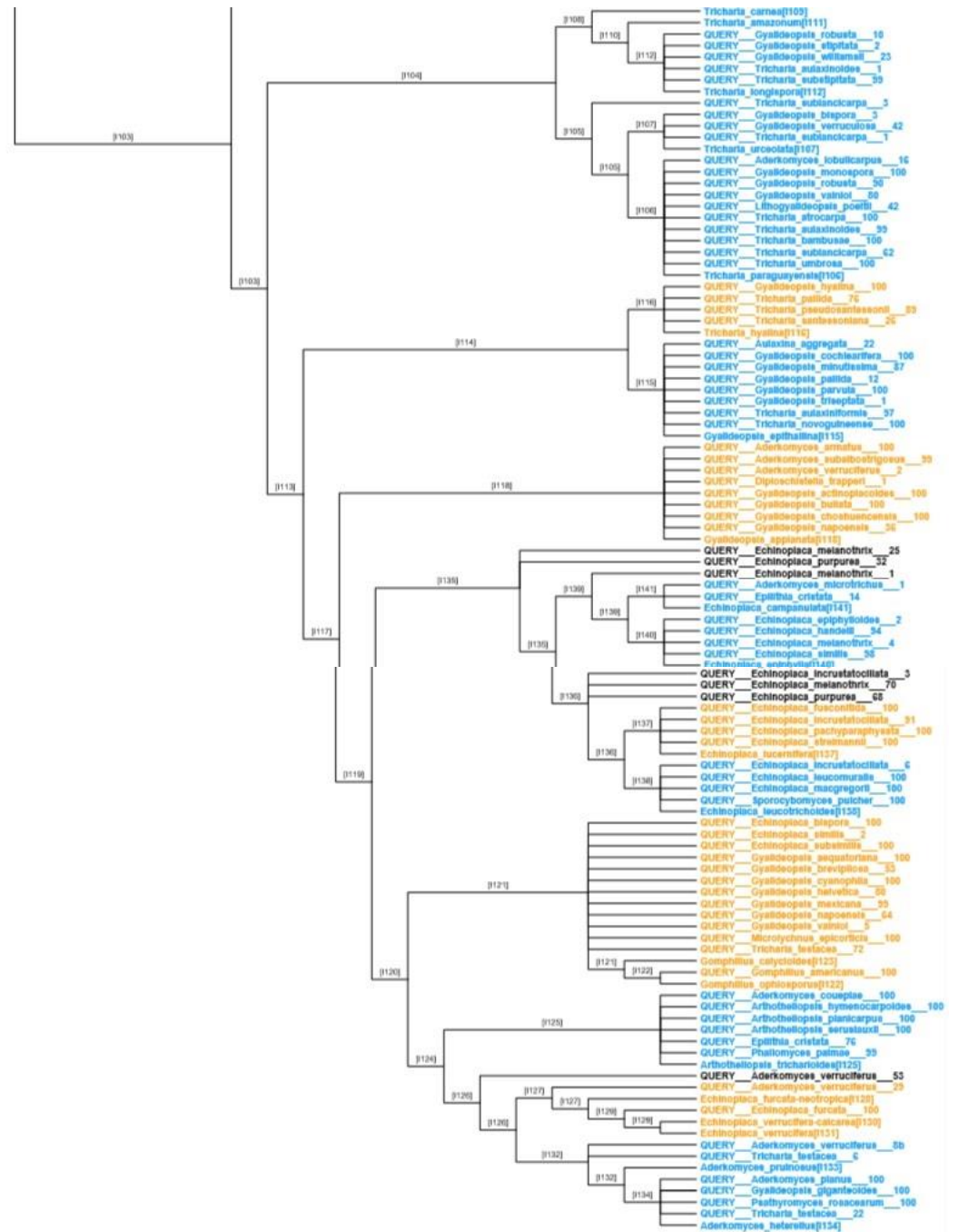


Figure 2–5: Result of the method of morphology-based phylogenetic binning using taxa in the molecular reference and taxa based on their phenotypic characters. The analysis include node identifications (ID) number and bootstrap support numbers after the query name from the RAxML analysis.

4. DISCUSSION

Gomphillaceae is a highly diverse family of lichenized fungi which is still not well understood in terms of its internal classification, species richness, and the usefulness of phenotype characters to delimit species. Studies on the 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; Xavier-Leite *et al.* 2018a), and molecular phylogenies, including our most recent study (Xavier-Leite *et al.* 2018b), are indication of the taxonomic diversity in the family.

This situation is comparable with Graphidaceae, which traditionally comprised 12 genera in two families and now contains 79 genera and well over 2000 species (Rivas Plata *et al.* 2012b; Lücking *et al.* 2017). Since genera are abstract entities, the number of genera distinguished in a group is subjective, as long as the taxa forming those are monophyletic, and should be based on practicality and some general rules. One possible rule is the species:genus ratio. In lichen fungi it is currently about 20:1 (Lücking *et al.* 2017), which is comparable to the ratio found in vascular plants but still higher than in most animal groups (Resh & McElravy 1993; Lenat & Resh 2001; Krug *et al.* 2008). 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 actually undersplit at the genus level. With the 42 genera now recognized in Gomphillaceae (Etayo 2017; Lücking *et al.* 2017; Xavier-Leite *et al.* 2018b, c), the current ratio for this family would be about 10:1, indicating oversplitting.

However, Gomphillaceae are much understudied and our phylogenetic analysis indicated considerable levels of cryptic speciation even in seemingly well-characterized taxa (Xavier-Leite *et al.* 2018b), so the true species richness is likely much higher than the currently recognized 418 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 knowledge and thus the average for Fungi in general.

As in Graphidaceae, the challenge with changing classifications based on molecular data, especially in groups where presumed key characters evolved multiple times independently, is the correct 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 allows for objective, testable predictions for the taxonomic placement of species for which no molecular data are available,

it is also susceptible to 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 of the non-foliicolous taxa sequenced, which make about one fourth of the family. As a consequence, particularly species of the genus *Gyalideopsis* 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 attempted to be binned at all. The binning approach therefore also helps to single out key taxa that need to be targeted for 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 the 17 newly recognized genus level clades in our previous molecular analysis (Xavier-Leite *et al.* 2018b), which also aided in the correct circumscription of these genera (Xavier-Leite *et al.* 2018c).

Thus far, the binning approach has not been used much in other studies, in addition to Graphidaceae and Lobariaceae also in some animal and plant groups (Springer *et al.* 2015; Testo *et al.* 2018). Most analyses were done in Graphidaceae, which helped considerable to 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 & Kalb 2018). The situation found in this family is comparable to that in Gomphillaceae, 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 (Rivas Plata *et al.* 2012b). However, binning cannot only be used to place species in genera, but also to assess diagnostic characters. The study by Parmen *et al.* (2012) helped to apply quantitative statistics to groups defined through binning to evaluate the highest level of phenotype discrimination among the proposed genera. This approach will also be useful for Gomphillaceae when more species have been sequenced.

An interesting study case to resolve a taxonomic problem by evaluating the placement of the type species through binning in Graphidaceae was *Leptotrema*, for which Lücking *et al.* (2015) found that the type species belonged in the genus *Myriotrema*, whereas the most common species, *L. wightii*, was unrelated and a new genus was established *Sanguinotrema*. A somewhat similar situation was found in Gomphillaceae, where Lücking *et al.* (2005) previously separated two similar genera, *Aderkomyces* and *Arthotheliopsis*, for a group of rather similar species. Our phylogenetic analysis showed that indeed the two clades are

related but apparently, the types of the two genera cluster in one of the clades based on the binning result, possibly requiring the description of a new genus for the other clade.

Thus, in 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 on a broad taxonomic level. It also clearly revealed the shortcomings of this approach in this case, with the need to obtain additional sequence data for the principally non-foliicolous taxa in the genera *Gyalidea* and *Gyalideopsis* s.lat. As a result, we provide an updated checklist of Gomphillaceae with revised genus assignments for each species (Supplemental Material 4).

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 for 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).

5. REFERENCES

- Aptroot, A., Lücking, R. 2002. Proposal to conserve *Gyalidea* (lichenized fungi: Asterothyriaceae, Ostropales) against an additional name, *Solorinella*. *Taxon* 51: 565.
- Berger, S.A., Krompaß, D. & Stamatakis, A. 2011a. Performance, accuracy and web-server for evolutionary placement of short sequence reads under maximum-likelihood. *Syst. Biol.* 60: 291–302.
- Berger, S.A., Stamatakis, A. & Lücking, A. 2011b. Morphologybased phylogenetic binning of the lichen genera *Allographa* and *Graphis* (Ascomycota: Graphidaceae) using molecular site weight calibration. *Taxon* 60:1450-1457.
- Dal-Forno, M., Lücking, R., Bungartz, F., Yáñez-Ayabaca, A., Marcelli, M.P., Spelmann, A.A., Coca, L.F., Chaves, J.L., Aptroot, A., Sipman, H.J.M., Sikaroodi, M., Gillevet, M., Lawrey, J.D. 2016. From one to six: unrecognized species diversity in the genus *Acantholichen* (lichenized Basidiomycota: Hygrophoraceae). *Mycologia* 108(1): 38–55.

- Dohrmann, M., Kelley, C., Kelly, M., Pisera, A., Hooper, J.N. and Reiswig, H.M., 2017. An integrative systematic framework helps to reconstruct skeletal evolution of glass sponges (Porifera, Hexactinellida). *Frontiers in zoology*, 14(1), p.18.
- Etayo, J. 2017. Hongos Liquenícolas de Ecuador. *Opera Lilloana* 50: 339.
- 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. and Gough, J., 2013. A daily-updated tree of (sequenced) life as a reference for genome research. *Scientific reports*, 3, p.2015.
- Grube, M., Baloch, E. & Lumbsch, H.T. 2004. The phylogeny of Porinaceae (Ostropomycetidae) suggests a neotenic origin of perithecia in Lecanoromycetes. *Mycol. Res.* 108: 1111–1118.
- 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.
- Hibbett, D.S., Binder, M., Bischoff, J.F., Blackwell, M., Cannon, P.F., Eriksson, O.E., Huhndorf, S., James, T., Kirk, P.M., Lücking, R., Lumbsch, H.T., Lutzoni, F., Matheny, P.B., McLaughlin, 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., Parmasto, 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*. *Mycol. Res.* 111: 509–547.
- 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., Kohlmeyer, J., Volkmann-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, I., Schultz, M., Yahr, R., Hibbett, D.S., Lutzoni, F., McLaughlin, D.J., Spatafora, J.W. & Vilgalys, R. 2006. Reconstructing the early evolution of Fungi using a six-gene phylogeny. *Nature* 443: 818–822.
- 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.
- Koch, M.A., Kiefer, M., German, D.A., Al-Shehbaz, I.A., Franzke, A., Mummehoff, K. and Schmickl, R., 2012. BrassiBase: Tools and biological resources to study characters and traits in the Brassicaceae—version 1.1. *Taxon* 61(5): 1001-1009.
- 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.
- 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* (Thelotremataceae), con un análisis filogenético. *Cryptogamie Mycologie* 20: 193–224.
- 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.
- Lücking, R. 2008. *Foliicolous Lichenized Fungi*. The New York Botanical Garden Press, pp. 873.
- Lücking, R. 2009. The taxonomy of the genus *Graphis* sensu Staiger (Ascomycota: Ostropales: Graphidaceae). *Lichenologist* 41: 319–362.
- Lücking, R., Archer, A.W. & Aptroot, A. 2009. A world-wide key to the genus *Graphis* (Ostropales: Graphidaceae). *Lichenologist* 41: 363–452.
- 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* 436–443pp.

- 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(4): 361-416.
- Lutzoni, F., Kauff, F., Cox, C., McLaughlin, 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.
- McLaughlin, 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.
- Moncada, B., Lücking, R. and Suárez, A., 2014. Molecular phylogeny of the genus *Sticta* (lichenized Ascomycota: Lobariaceae) in Colombia. *Fungal Diversity* 64(1): 205-231.
- Parnmen S, Lücking R, Lumbsch HT. 2012b. Phylogenetic classification at generic level in the absence of distinct phylogenetic patterns of phenotypical variation: a case study in Graphidaceae (Ascomycota). *PLoS ONE* 7: 1–13.
- Resh, V.H., McElravy, E.P. 1993. Contemporary quantitative approaches to biomonitoring using benthic macroinvertebrates. In: Rosenberg, D.M., Resh, V.H. Fresh-water biomonitoring and benthic macroinvertebrates. *Chapman and Hall*, New York, 159-194p.
- Rivas Plata, E., Hernández, J.E., Lücking, R., Staiger, B., Kalb, K., Cáceres, M.E.S. 2011a. *Graphis* is two genera – A remarkable case of parallel evolution in lichenized Ascomycota. *Taxon* 60: 99–107.
- Rivas-Plata, E., Lumbsch, H.T. 2011b. Parallel evolution and phenotypic divergence in lichenized fungi: A case study in the lichen-forming fungal Family Graphidaceae (Ascomycota: Lecanoromycetes: Ostropales). *Molecular Phylogenetics and Evolution* 61: 45-63.
- Rivas Plata, E., Lücking, R., Lumbsch, H.T. 2012a. A new classification for the Family Graphidaceae s. lat. (Ascomycota: Lecanoromycetes: Ostropales). *Fungal Diversity* 52(1): 107-121.

- Rivas Plata E, Lücking R, Lumbsch H.T. 2012b. Molecular phylogeny and systematics of the Ocellularia clade (Ascomycota: Ostropales: Graphidaceae). *Taxon* 61 (6): 1161–1179.
- Rivas Plata, E., Parmen, 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.
- Spatafora, J.W., Y. Chang, G.L. Benny, K. Lazarus, M.E. Smith, M.L. Berbee, G. Bonito, N. Corradi, I. Grigoriev, A. Gryganskyi, and T.Y. James. 2016. A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. *Mycologia* 108: 1028–1046.
- 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.
- 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.
- Vězda, A. 1973. Foliicole Flechten aus der Republik Guinea (W.–Afrika). I. *Acta Musei Silesiae, Opava* 22: 67–90.
- Vězda, 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., Lumbsch, H.T., Liu, J.K., Maharachchikumbura, S.S., Ekanayaka, A.H., Tian, Q. and Phookamsak, R., 2018. Outline of Ascomycota: 2017. *Fungal Diversity* 88: 167-263.
- Xavier-Leite, A.B., Cáceres, M.E.S., Goto, B.T., Lücking, R. 2018a. The genus *Gyalideopsis* (lichenized Ascomycota: Gomphillaceae) in Brazil: updated checklist, key to species, and two novel taxa with unique hyphophores. *The Bryologist* 121(1): 032–040.
- Xavier-Leite, A.B., Cáceres, M.E.S., Moncada, B., Lücking, R., Goto, B.T. 2018b. A phylogenetic revision of the classification of the lichenized family Gomphillaceae (Ascomycota: Ostropales), in prep.

Xavier-Leite, A.B., Goto, B.T., Lücking, R., Cáceres, M.E.S. 2018c. New genera in the lichenized family Gomphillaceae (Ascomycota: Ostropales) delimited by integrating molecular phylogeny with phenotypic characters, in prep.

Supplemental Material 1.

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. Node identifications (ID) are listed for each node and the final genus placement is indicated for each species. Genus placement is consistent for a taxon and therefore might not be the same as Node ID in alternative node placements with low support. In cases where the placement was not resolved or some conflict was detected, we adopted a conservative genus placement which is indicated in brackets.

Taxon	Node	Supp.	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 hymenocarpoides</i>	I125	100	<i>Arthotheliopsis</i>	<i>Aderkomyces</i>
<i>Arthotheliopsis planicarpus</i>	I125	100	<i>Arthotheliopsis</i>	<i>Aderkomyces</i>
<i>Arthotheliopsis serusiauxii</i>	I125	100	<i>Arthotheliopsis</i>	<i>Aderkomyces</i>
<i>Arthotheliopsis tricharioides</i>	I125	[ref]	<i>Arthotheliopsis</i>	<i>Aderkomyces</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 atromarginatum</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 gigantosporum</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>
<i>Asterothyrium segmentatum</i>	I19	81	<i>Asterothyrium-Linhartia</i>	[<i>Asterothyrium</i>]
<i>Asterothyrium segmentatum</i>	I26	19	<i>Asterothyrium</i>	[<i>Asterothyrium</i>]
<i>Asterothyrium septemseptatum</i>	I26	100	<i>Asterothyrium</i>	<i>Asterothyrium</i>
<i>Asterothyrium subargenteum</i>	I27	100	<i>Asterothyrium</i>	<i>Asterothyrium</i>
<i>Asterothyrium tetrasporum</i>	I25	99	<i>Asterothyrium</i>	<i>Asterothyrium</i>
<i>Asterothyrium tetrasporum</i>	I24	1	<i>Asterothyrium</i>	<i>Asterothyrium</i>
<i>Asterothyrium umbilicatum</i>	I31	100	<i>Psorotheciopsis</i>	[<i>Asterothyrium</i>]
<i>Asterothyrium uniseptatum</i>	I25	100	<i>Asterothyrium</i>	<i>Asterothyrium</i>
<i>Asterothyrium vezdae</i>	I26	100	<i>Asterothyrium</i>	<i>Asterothyrium</i>
<i>Aulaxina aggregata</i>	I45	78	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina aggregata</i>	I115	22	<i>Adelphomyces</i>	<i>Aulaxina</i>
<i>Aulaxina corticola</i>	I44	100	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina dictyospora</i>	I50	100	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina epiphylla</i>	I45	100	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina intermedia</i>	I49	[ref]	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina microphana</i>	I44	99	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina microphana</i>	I42	1	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina minuta</i>	I41	[ref]	<i>Aulaxinella</i>	<i>Aulaxinella</i>
<i>Aulaxina multiseptata</i>	I44	100	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina opegraphina</i>	I45	[ref]	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina quadrangula</i>	I47	[ref]	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina submuralis</i>	I50	[ref]	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Aulaxina uniseptata</i>	I41	100	<i>Aulaxinella</i>	<i>Aulaxinella</i>
<i>Aulaxina unispora</i>	I45	100	<i>Aulaxina</i>	<i>Aulaxina</i>
<i>Bullatina aspidota</i>	I75	[ref]	<i>Bullatina</i>	[<i>Calenia</i>]
<i>Calenia africana</i>	I86	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia applanata</i>	I90	100	<i>Actinoplaca</i>	[<i>Aplanocalenia</i>]
<i>Calenia areolata</i>	I79	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia bullatinoides</i>	I88	[ref]	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia depressa</i>	I96	[ref]	<i>Calenia-Echinoplaca</i> grade	<i>Calenia</i>
<i>Calenia dictyospora</i>	I76	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]

<i>Calenia echinoplacoides</i>	I86	99	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia echinoplacoides</i>	I73	1	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia flava</i>	I77	90	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia flava</i>	I97	5	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia flava</i>	I96	4	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia flava</i>	I79	1	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia fumosa</i>	I86	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia graphidea</i>	I84	[ref]	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia inconspicua</i>	I77	43	<i>Calenia-Echinoplaca</i> grade	<i>Aplanocalenia</i>
<i>Calenia inconspicua</i>	I16	32	<i>Monocalenia</i>	<i>Aplanocalenia</i>
<i>Calenia inconspicua</i>	I18	16	<i>Monocalenia</i>	<i>Aplanocalenia</i>
<i>Calenia inconspicua</i>	I90	9	<i>Actinoplaca</i>	<i>Aplanocalenia</i>
<i>Calenia leptocarpa</i>	I96	49	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia leptocarpa</i>	I77	40	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia leptocarpa</i>	I80	9	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia leptocarpa</i>	I98	2	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia lobulata</i>	I73	[ref]	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia lueckingii</i>	I82	[ref]	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia maculans</i>	I39	100	<i>Caleniella</i>	<i>Caleniella</i>
<i>Calenia microcarpa</i>	I58	100	<i>Gyalectidium</i>	<i>Gyalectidium</i>
<i>Calenia minuta</i>	I89	86	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia minuta</i>	I88	11	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia minuta</i>	I91	3	<i>Veزدamyces</i>	[<i>Calenia</i>]
<i>Calenia monospora</i>	I18	[ref]	<i>Monocalenia</i>	<i>Monocalenia</i>
<i>Calenia obtecta</i>	I76	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia philippinensis</i>	I79	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia phyllogena</i>	I97	[ref]	<i>Calenia-Echinoplaca</i> grade	<i>Calenia</i>
<i>Calenia pruinosa</i>	I73	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia rionigrensis</i>	I79	100	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia rolandiana</i>	I16	86	<i>Monocalenia</i>	<i>Monocalenia</i>
<i>Calenia rolandiana</i>	I28	14	unresolved	<i>Monocalenia</i>
<i>Calenia solorinoides</i>	I17	[ref]	<i>Pseudocalenia</i>	<i>Pseudocalenia</i>
<i>Calenia subdepressa</i>	I86	53	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia subdepressa</i>	I79	47	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia submuralis</i>	I79	[ref]	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia thelotremella</i>	I79	97	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]

<i>Calenia thelotremella</i>	I97	3	<i>Calenia-Echinoplaca</i> grade	[<i>Calenia</i>]
<i>Calenia triseptata</i>	I39	[ref]	<i>Caleniella</i>	<i>Caleniella</i>
<i>Calenia viridis</i>	I18	100	<i>Monocalenia</i>	<i>Monocalenia</i>
<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 leprieurii</i>	I146	[ref]	<i>outgroup</i>	[<i>outgroup</i>]
<i>Coenogonium luteum</i>	I143	[ref]	<i>outgroup</i>	[<i>outgroup</i>]
<i>Coenogonium pineti</i>	I145	[ref]	<i>outgroup</i>	[<i>outgroup</i>]
<i>Diploschistella athalloides</i>	I14	50	<i>Serusiauxiella</i>	[<i>Diploschistella</i>]
<i>Diploschistella athalloides</i>	I32	50	<i>Gyalidea</i>	[<i>Diploschistella</i>]
<i>Diploschistella lithophila</i>	I14	57	<i>Serusiauxiella</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>calcareo</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>
<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 yahriae</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 bispora</i>	I1	97	unresolved	[<i>Gyalideopsis</i>]
<i>Gyalideopsis bispora</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	<i>outgroup</i>	[<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	<i>outgroup</i>	[<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	<i>outgroup</i>	[<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>]
<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>Serusiauxiella</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>Veزدamyces</i>	[<i>Gyalideopsis</i>]
<i>Gyalideopsis montana</i>	I11	31	<i>Roselviria</i>	[<i>Gyalideopsis</i>]
<i>Gyalideopsis montana</i>	I93	5	<i>Veزدamyces</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	<i>outgroup</i>	[<i>Gyalideopsis</i>]

<i>Gyalideopsis piceicola</i>	I1	95	unresolved	[<i>Gyalideopsis</i>]
<i>Gyalideopsis piceicola</i>	I142	5	<i>outgroup</i>	[<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>Serusiauxiella</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>
<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	<i>outgroup</i>	[<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 variaseptata</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 vivantii</i>	I32	98	<i>Gyalidea</i>	[<i>Lithogyalideopsis</i>]
<i>Lithogyalideopsis vivantii</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>Serusiauxiella</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 conspersa</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>Serusiauxiella</i>	<i>Serusiauxiella</i>
<i>Tricharia hyalina</i>	I116	[ref]	<i>Batistomyces</i>	<i>Batistomyces</i>
<i>Tricharia kashiwadanii</i>	I70	70	unresolved	<i>Microxyphiomyces</i>
<i>Tricharia kashiwadanii</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>Roselviria</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>Serusiauxiella</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>
<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>Roselviria</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>]

Supplemental Material 2. 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 Supplemental Material 4); added characters are marked with asterisks at their place of insertion.

(1) Ecology (14)

Lichenization

1 Lichenization: 0 = pre / 1 = abs (lichenicolous)

Substrate.—Includes taxa attacked by lichenicolous species.

2 Anorganic: 0 = abs / 1 = pre

3 Organic: 0 = abs / 1 = pre

4 Leaves: 0 = abs / 1 = pre

5 *Gomphillaceae*: 0 = abs / 1 = pre

6 *Pilocarpaceae*: 0 = abs / 1 = pre

Habitat and microsite.—Where taxon is most commonly found.

7 In tropical climates: 0 = abs / 1 = pre

8 In tropical montane climates: 0 = abs / 1 = pre

9 In tropical alpine climates: 0 = abs / 1 = pre

10 In subtropical climates: 0 = abs / 1 = pre

11 In temperate climates: 0 = abs / 1 = pre

12 In sheltered microsites: 0 = abs / 1 = pre

13 In semi-exposed microsites: 0 = abs / 1 = pre

14 In fully exposed microsites: 0 = abs / 1 = pre

(2) Thallus morphology and anatomy (46)

Thallus shape and size.—Size refers to entire thallus, not individual elements.

15 Dispersed: 0 = abs / 1 = pre

16 Smaller than 1 mm: 0 = abs / 1 = pre

17 Larger than 3 mm: 0 = abs / 1 = pre

18 Convex elements: 0 = abs / 1 = pre

19 Bullate elements: 0 = abs / 1 = pre

Thallus surface structure

20 Small verrucae: 0 = abs / 1 = pre

21 Large verrucae: 0 = abs / 1 = pre

22 Radiate ridges: 0 = abs / 1 = pre

- 23 Areoles: 0 = abs / 1 = pre
 24 Papillae: 0 = abs / 1 = pre
 25 Thick white layer: 0 = abs / 1 = pre

Thallus surface color.—A blend of colors can be present in a taxon.

- 26 Green: 0 = abs / 1 = pre
 27 Grey: 0 = abs / 1 = pre
 28 White: 0 = abs / 1 = pre
 29 Yellow: 0 = abs / 1 = pre
 30 Glossiness: 0 = abs / 1 = pre
 31 Marginal zonation: 0 = abs / 1 = pre

Prothallus.—Prothallus can be translucent, white or dark. Translucent is default if prothallus is present (1/0/0).

- 32 Non-algiferous prothallus: 0 = abs / 1 = pre
 33 White: 0 = abs / 1 = pre
 34 Dark: 0 = abs / 1 = pre

Thallus crystals.—Several taxa contain crystals in the thallus or on the thallus surface that are not calcium oxalate crystals (e.g. needle-shaped crystals in the *Echinoplaca furcata* group or irregular crystals causing the pruina in the *E. atrofusca* group). These have been termed according to the group where they occur.

- 35 Calcium oxalate: 0 = abs / 1 = pre
 36 'furcata' type: 0 = abs / 1 = pre
 37 'atrofusca' type: 0 = abs / 1 = pre
 38 'papillifera' type: 0 = abs / 1 = pre

Thallus cortex.—Most taxa have a cartilaginous, corticiform layer of strongly appressed, parallel hyphae.

- 39 Corticiform layer: 0 = abs / 1 = pre
 40 Cellular cortex: 0 = abs / 1 = pre
 * Cellular cortex: 0 = irregular arrangement / 1 = radiating cell rows

Sterile setae.—We distinguished between taxa in which setae are always present (e.g. *Tricharia sensu stricto*, most *Aderkomyces*) and those in which setae can be absent or present (most *Echinoplaca* and *Calenia* species).

- 41 Sterile setae: 0 = abs / 1 = pre
 42 Sterile setae (always present): 0 = abs / 1 = pre
 43 On thallus: 0 = abs / 1 = pre
 44 Clustered around apothecia: 0 = abs / 1 = pre
 45 On prothallus: 0 = abs / 1 = pre

Sterile setae color

46 Redbrown: 0 = abs / 1 = pre

47 Black: 0 = abs / 1 = pre

Sterile setae structure and shape.—Setae can be curved and bent and do not break when manipulated with care, or setae are straight and stiff and easily break when manipulated. Setae shorter than 0.5 mm are the default.

48 Stiffness: 0 = abs / 1 = pre

49 Calcium oxalate crystals: 0 = abs / 1 = pre

50 Longer than 0.5 mm: 0 = abs / 1 = pre

51 Longer than 1.0 mm: 0 = abs / 1 = pre

52 Lateral ramifications: 0 = abs / 1 = pre

53 Apical ramifications: 0 = abs / 1 = pre

Sterile setae second type.—Distinguished when two types of setae are present on the same thallus.

54 Sterile setae second type: 0 = abs / 1 = pre

Sterile setae second type color

55 Redbrown: 0 = abs / 1 = pre

56 Black color: 0 = abs / 1 = pre

Sterile setae second type structure and shape

57 Shorter than 0.5 mm: 0 = abs / 1 = pre

58 Longer than 1. mm: 0 = abs / 1 = pre

Soralia occurrence

59 Soralia: 0 = abs / 1 = pre

(3) Apothecial morphology and anatomy (86)

Apothecia occurrence

60 Apothecia: 0 = abs / 1 = pre

Apothecia shape and size.—Apothecia smaller than 0.3 mm is the default.

61 Basal stipe: 0 = abs / 1 = pre

62 Basal constriction: 0 = abs / 1 = pre

63 Strong horizontal growth: 0 = abs / 1 = pre

64 Strong vertical growth: 0 = abs / 1 = pre

65 Level with thallus surface: 0 = abs / 1 = pre

66 Immersion: 0 = abs / 1 = pre

67 Angular outline: 0 = abs / 1 = pre

68 Lobular outline: 0 = abs / 1 = pre

69 Lirelliform elongation: 0 = abs / 1 = pre

70 Aggregation: 0 = abs / 1 = pre

71 Apothecia > 0.3 mm: 0 = abs / 1 = pre

72 Apothecia > 0.8 mm: 0 = abs / 1 = pre

Apothecia disc color

73 White: 0 = abs / 1 = pre

74 Yellow: 0 = abs / 1 = pre

75 Red: 0 = abs / 1 = pre

76 Brown: 0 = abs / 1 = pre

77 Grey: 0 = abs / 1 = pre

78 Black: 0 = abs / 1 = pre

79 Green: 0 = abs / 1 = pre

80 Dark coloration: 0 = abs / 1 = pre

81 Translucence: 0 = abs / 1 = pre

Apothecia disc structure and shape

82 Convexity: 0 = abs / 1 = pre

83 Concavity: 0 = abs / 1 = pre

84 Pruina: 0 = abs / 1 = pre

85 Pruina dark pigment: 0 = abs / 1 = pre

Apothecia thalline margin.—Three types of margins are distinguished: thalline rim in addition to well-developed proper margin (not fused); thin thalline lobules formed by cortex in addition to well-developed proper margin (not fused); and algiferous thalline margin fused with and covering reduced proper margin.

86 Non-algiferous thalline rim: 0 = abs / 1 = pre

87 Non-algiferous lobules: 0 = abs / 1 = pre

88 Algiferous margin: 0 = abs / 1 = pre

* Algiferous margin: 0 = entire / 1 = lobulate

89 Slight prominence: 0 = abs / 1 = pre

90 Strong prominence: 0 = abs / 1 = pre

91 Carbonization: 0 = abs / 1 = pre

Apothecia proper margin

92 Thin in young apothecia: 0 = abs / 1 = pre

93 Thick in young apothecia: 0 = abs / 1 = pre

94 Thin in mature apothecia: 0 = abs / 1 = pre

95 Thick in mature apothecia: 0 = abs / 1 = pre

96 Prominence: 0 = abs / 1 = pre

97 Formation of teeth or lobes: 0 = abs / 1 = pre

98 Basal-lateral expansion: 0 = abs / 1 = pre

99 Color different from disc: 0 = abs / 1 = pre

100 Paler: 0 = abs / 1 = pre

101 Darker: 0 = abs / 1 = pre

102 Black: 0 = abs / 1 = pre

103 Pruina: 0 = abs / 1 = pre

104 Pruina dark pigment: 0 = abs / 1 = pre

Excipulum.—The default is a hyphal excipulum composed of branched hyphae embedded in a gelatinous matrix (107=0/108=0).

105 Columella: 0 = abs / 1 = pre

106 Well-developed excipulum: 0 = abs / 1 = pre

107 Prosoplectenchymatous: 0 = abs / 1 = pre

108 Paraplectenchymatous: 0 = abs / 1 = pre

109 Slight pigmentation: 0 = abs / 1 = pre

110 Strong pigmentation: 0 = abs / 1 = pre

111 Fissure at thalline margin: 0 = abs / 1 = pre

Hypothecium, epithecium and hymenium.—For asci, the default are clavate asci (120=0/121=0).

112 Well-developed hypothecium: 0 = abs / 1 = pre

113 Slight pigmentation: 0 = abs / 1 = pre

114 Strong pigmentation: 0 = abs / 1 = pre

115 Well-developed epithecium: 0 = abs / 1 = pre

116 Strong pigmentation: 0 = abs / 1 = pre

117 Epithecial algae: 0 = abs / 1 = pre

118 Paraphyses ramifications: 0 = abs / 1 = pre

119 Paraphyses anastomoses: 0 = abs / 1 = pre

120 Cylindrical asci: 0 = abs / 1 = pre

121 Ovoid asci: 0 = abs / 1 = pre

Ascospores number.—The default is 8 ascospores per ascus (0/0/0/0/0).

122 Degeneration of 0: 0 = abs (8) / 1 = pre (1-8)

123 Degeneration of 2: 0 = abs (6-8) / 1 = pre (1-6)

124 Degeneration of 4: 0 = abs (4-6) / 1 = pre (2-4)

125 Degeneration of 6: 0 = abs (2-4) / 1 = pre (1-2)

126 Degeneration of 7: 0 = abs (1-2) / 1 = pre (1)

127 Polyspory: 0 = abs / 1 = pre

Ascospores septation.—The default are 1-septate ascospores (0/0/0/0/0).

128 More than 1 transverse: 0 = abs / 1 = pre

129 More than 3 transverse: 0 = abs / 1 = pre

130 More than 7 transverse: 0 = abs / 1 = pre

131 More than 15 transverse: 0 = abs / 1 = pre

132 0–3 longitudinal: 0 = abs / 1 = pre (submur.)

133 3–7 longitudinal: 0 = abs / 1 = pre (muriform)

Ascospores shape and size.—The default are ellipsoid ascospores less than 10 µm long.

134 Vermiform: 0 = abs / 1 = pre

135 Filiform-acicular: 0 = abs / 1 = pre

136 Ovoid: 0 = abs / 1 = pre

137 Longer than 10 µm: 0 = abs / 1 = pre

138 Longer than 20 µm: 0 = abs / 1 = pre

138 Longer than 30 µm: 0 = abs / 1 = pre

140 Longer than 50 µm: 0 = abs / 1 = pre

141 Spiral distortion: 0 = abs / 1 = pre

142 Apical widening: 0 = abs / 1 = pre

* Septa thickening: 0 = abs / 1 = pre

* Wall thickening: 0 = abs / 1 = pre

(4) Hyphophores (67)

Hyphophores occurrence

143 Hyphophores: 0 = abs / 1 = pre

144 Marginal on thallus: 0 = abs / 1 = pre

145 On prothallus: 0 = abs / 1 = pre

Hyphophore type.—Four main types are distinguished: setiform, isidioid lacking stipe, squamiform, and isidioid-'thlasidioid'. The default is setiform (0/0/0); isidioid is (1/0/0), squamiform is (1/1/0), and 'thlasidioid' is (1/0/1).

146 Setiform type: 0 = pre / 1 = abs – DUVIDA

+++ Setiform white: 0 = abs / 1 = abs

147 Squamiform type: 0 = abs / 1 = pre

148 'Thlasidioid' type: 0 = abs / 1 = pre

Stipe size.—The default size is 0.5–1.0 mm. In some taxa, the stipe is completely reduced, but their hyphophore structure is the same as those with stipe and widened upper part; these are different from the squamiform type and thus coded differently (as setiform with reduced stipe).

149 Longer than 1.0 mm: 0 = abs / 1 = pre

150 Shorter than 0.5 mm: 0 = abs / 1 = pre

151 Reduction: 0 = abs / 1 = pre

Diahyphal bunch position.—The default is apical-lateral (0/0).

152 Subapical: 0 = abs / 1 = pre

153 Capitata: 0 = abs / 1 = pre

Setiform hyphophore apex shape.—The default is bristle-shaped, with no differentiated apical part. Coronate means a corona-like expansion (e.g. *Gyalideopsis monospora*).

- 154 Acute: 0 = abs / 1 = pre
 155 Thickened: 0 = abs / 1 = pre
 156 Widened: 0 = abs / 1 = pre
 157 Lanceolate: 0 = abs / 1 = pre
 158 Spatulate: 0 = abs / 1 = pre
 159 Arrow-shaped: 0 = abs / 1 = pre
 160 Mussle-shaped: 0 = abs / 1 = pre
 161 Hand-shaped: 0 = abs / 1 = pre
 162 Hooked: 0 = abs / 1 = pre
 163 Coronate: 0 = abs / 1 = pre
 164 Umbellate: 0 = abs / 1 = pre

Basal pigmentation: 0 = abs / 1 = pre

- 166 Apical pigmentation: 0 = abs / 1 = pre
 167 Carbonization: 0 = abs / 1 = pre
 168 Calcium oxalate crystals: 0 = abs / 1 = pre
 169 Hairs or tomentum: 0 = abs / 1 = pre

Squamiform hyphophore scale shape.—Applies only to taxa with truly squamiform hyphophores and those derived from this type (e.g. *Gyalectidium*). The default are vertical scales with entire margin and white color.

- 170 Scale: 0 = abs / 1 = pre
 171 Division into subscales: 0 = abs / 1 = pre
 172 Widened: 0 = abs / 1 = pre
 173 Strongly widened: 0 = abs / 1 = pre
 174 Narrowed: 0 = abs / 1 = pre
 175 Division into setae: 0 = abs / 1 = pre
 176 Campylidioid: 0 = abs / 1 = pre
 177 Apex acute: 0 = abs / 1 = pre
 178 Apex with horns: 0 = abs / 1 = pre
 179 Apex dentate: 0 = abs / 1 = pre
 180 Oblique orientation: 0 = abs / 1 = pre
 181 Horizontal orientation: 0 = abs / 1 = pre
 182 Translucity: 0 = abs / 1 = pre
 183 Dark pigmentation: 0 = abs / 1 = pre

'Thlasidioid' hyphophores shape and color.—Applies only to taxa with truly 'thlasidioid' hyphophores (*Gyalideopsis anastomosans* group).

- 184 Lateral expansion: 0 = abs / 1 = pre
 185 Dark pigment: 0 = abs / 1 = pre

Diahyphal mass shape.—The diahyphal mass may be drop-shaped and entire (default) or divided into several entities hold together or lacking a gelatinous matrix (checked under the microscope under low pressure). The hyphal cord refers to the presence of basal, unbranched, agglutinated hyphae connecting the branched diahyphae with the supporting stipe (can be interpreted as flexible, divided extension of the stipe now forming part of the diahyphae).

- 186 Bell-shaped: 0 = abs / 1 = pre
- 187 Globose: 0 = abs / 1 = pre
- 188 Applanate: 0 = abs / 1 = pre
- 189 Disc-shaped: 0 = abs / 1 = pre
- 190 Division into subelements: 0 = abs / 1 = pre
- 191 Gelatinous matrix: 0 = pre / 1 = abs
- 192 Hyphal cord: 0 = abs / 1 = pre

Diahyphae structure.—The default are branched hyphae lacking constrictions (filiform) and hence being most similar to undifferentiated mycelium hyphae. Constrictions can be found only in the apical portion of the diahyphae or throughout (partially or entirely moniliform). Branching might be restricted to the base of the diahyphae (common in the filiform type), and the apical sections or cells might be slightly to strongly differentiated in shape and even resemble true conidia. In moniliform diahyphae, the default are clavate-fusiform segments, but several taxa have distinctly bacillar or sausage-shaped cells. In the *Echinoplaca lucernifera* group, two types of diahyphae are present; the second type is termed 'lucernifera' type hyphae.

- 193 Constrictions (apical)- monili: 0 = abs / 1 = pre
- 194 Constrictions (throughout)- m: 0 = abs / 1 = pre
- 195 Bacillar segments: 0 = abs / 1 = pre
- 196 Thickened hyphae: 0 = abs / 1 = pre
- 197 Basal branching only - filif: 0 = abs / 1 = pre
- 198 Slight apical differentiation: 0 = abs / 1 = pre
- 199 Strong apical differentiation: 0 = abs / 1 = pre
- 200 Spermatozoid end segments: 0 = abs / 1 = pre
- 201 Branched end segments: 0 = abs / 1 = pre
- 202 Fusiform end segments: 0 = abs / 1 = pre
- 203 Flagelliform end segments: 0 = abs / 1 = pre
- 204 1–3-septate end segments: 0 = abs / 1 = pre
- 205 Multiseptate end segments: 0 = abs / 1 = pre
- 206 Constricted end segments: 0 = abs / 1 = pre
- 207 Flagelliform appendages: 0 = abs / 1 = pre
- 208 'lucernifera' type hyphae: 0 = abs / 1 = pre
- 209 Associated algal cells: 0 = abs / 1 = pre

(5) Pycnidial morphology and anatomy (10)

- * Pycnidia presence: 0 = abs / 1 = pre
- * Pycnidia position: 0 = laminal / 1 = marginal
- * Pycnidia color: 0 = pale / 1 = carbonized (black)
- * Pycnidia beak: 0 = absent / 1 = present
- * Pycnidia shape: 0 = conical to wart-shaped / 1 = applanate
- * Conidia shape: 0 = bacillar to elongate / 1 = filiform
- * Conidia septa: 0 = absent / 1 = present
- * Conidia length: 0 = up to 10 um / 1 = 10-20 um
- * Conidia length: 0 = up to 20 um / 1 = 20-30 um
- * Conidia length: 0 = up to 30 um / 1 = 30-50 um

Supplemental Material 3. Checklist of Gomphillaceae with the taxa used in the phenotype-based phylogenetic binning marked with one asterisk and those included in the molecular study and the binning (as reference taxa) with two asterisks.

Actinoplaca Müll. Arg. (2 species)

≡ *Actinoplacomycetes* Cif. & Tomas.

**Actinoplaca gemmifera* (Lücking) Lücking, Sérus. & Vězda

≡ *Echinoplaca gemmifera* Lücking

***Actinoplaca strigulacea* Müll. Arg.

≡ *Actinoplacomycetes strigulaceae* Cif. & Tomas.

≡ *Echinoplaca strigulacea* (Müll. Arg.) R. Sant.

= *Actinoplaca strigulacea* var. *discreta* Müll. Arg.

Adelphomyces Xavier-Leite, M. Cáceres & Lücking (3 species)

**Adelphomyces cochlearifer* (Lücking & Sérus.) Xavier-Leite, M. Cáceres & Lücking

≡ *Gyalideopsis cochlearifera* Lücking & Sérus.

***Adelphomyces epithallina* (Lücking) Xavier-Leite, M. Cáceres & Lücking

≡ *Gyalideopsis epithallina* Lücking

**Adelphomyces parvulus* (Hafellner & Vězda) Xavier-Leite, M. Cáceres & Lücking

≡ *Gyalideopsis parvula* Hafellner & Vězda

Aderkomyces Bat. (17 species)

**Aderkomyces armatus* (Vězda) Lücking, Sérus. & Vězda

≡ *Tricharia armata* Vězda

**Aderkomyces couepiae* Bat.

Tricharia couepiae (Bat.) Lücking & Sérus.

**Aderkomyces cretaceus* (Vězda) Lücking, Sérus. & Vězda

≡ *Tricharia cretacea* Vězda

**Aderkomyces cubanus* (Vězda) Lücking, Sérus. & Vězda

≡ *Tricharia cubana* Vězda

**Aderkomyces dilatatus* (Vězda) Lücking, Sérus. & Vězda

≡ *Tricharia dilatata* Vězda

**Aderkomyces fumosus* (Kalb & Vězda) Lücking, Sérus. & Vězda

≡ *Tricharia fumosa* Kalb & Vězda

Aderkomyces gomezii Lücking

**Aderkomyces microtrichus* (Lücking & Kalb) Lücking, Sérus. & Vězda

≡ *Tricharia microtricha* Lücking & Kalb

***Aderkomyces papilliferus* (Lücking) Lücking, Sérus. & Vězda

≡ *Tricharia papillifera* Lücking

**Aderkomyces ramiferus* (Sérus.) Lücking, Sérus. & Vězda

≡ *Tricharia ramifera* Sérus.

Aderkomyces rigidus Lücking & Sipman

Aderkomyces sikkimensis Pinokiyo, Kr.P. Singh & Lücking

**Aderkomyces subalbostrigosus* (Lücking) Lücking, Sérus. & Vězda

≡ *Tricharia subalbostrigosa* Lücking

**Aderkomyces subplanus* (Kalb & Vězda) Lücking, Sérus. & Vězda

≡ *Tricharia subplana* Kalb & Vězda

Aderkomyces testaceus (Kalb & Vězda) Lücking, Sérus. & Vězda

≡ *Tricharia testacea* Kalb & Vězda

Aderkomyces thailandicus Papong, Boonpr. & Lücking

**Aderkomyces verruciferus* (Lücking) Lücking, Sérus. & Vězda

≡ *Tricharia verrucifera* Lücking

Aplanocalenia Lücking, Sérus. & Vězda (1 species)

**Aplanocalenia inconspicua* (Müll. Arg.) Lücking, Sérus. & Vězda

≡ *Calenia inconspicua* (Müll. Arg.) R. Sant. & Lücking

Aptrootidea Xavier-Leite, M. Cáceres & Lücking (6 species)

**Aptrootidea amapensis* (Bat. & Poroca) Xavier-Leite, M. Cáceres & Lücking

≡ *Echinoplaca amapensis* Bat. & Poroca

**Aptrootidea atrofusca* (R. Sant.) Xavier-Leite, M. Cáceres & Lücking

≡ *Echinoplaca atrofusca* R. Sant.

**Aptrootidea atromuralis* (Lücking) Xavier-Leite, M. Cáceres & Lücking

≡ *Echinoplaca atromuralis* Lücking

***Aptrootidea marginata* (Lücking) Xavier-Leite, Cáceres & Lücking

≡ *Echinoplaca marginata* Lücking

**Aptrootidea triseptata* (Lücking) Xavier-Leite, M. Cáceres & Lücking

≡ *Echinoplaca triseptata* Lücking

**Aptrootidea wilsoniorum* (Lücking) Xavier-Leite, M. Cáceres & Lücking

≡ *Echinoplaca wilsoniorum* Lücking

≡ *Echinoplaca wilsonii* Lücking

Arthotheliopsis Vain. (4 species)

≡ *Arthotheliopsisidomyces* Cif. & Tomas.

= *Phallomyces* Bat. & Valle

Arthotheliopsis floridensis Lücking & W.R. Buck

**Arthotheliopsis hymenocarpoides* Vain.

≡ *Arthotheliopsisidomyces hymenocarpoidis* Cif. & Tomas.

≡ *Echinoplaca hymenocarpoides* (Vain.) Lücking

= *Phallomyces palmae* Bat. & Valle

**Arthotheliopsis serusiauxii* (Lücking) Lücking, Sérus. & Vězda

≡ *Echinoplaca serusiauxii* Lücking

***Arthotheliopsis tricharioides* (Kalb & Vězda) Lücking, Sérus. & Vězda

≡ *Echinoplaca tricharioides* Kalb & Vězda

Asterothyrium Müll. Arg. (31 species, plus 1 infraspecies)

≡ *Asterothyriomyces* Cif. & Tomas.

= *Actinoteichus* Cavalc. & Poroca

= *Diplopeltopsis* Henn. ex Höhn.

= *Lopadiopsisidomyces* Cif. & Tomas.

= *Lopadiopsis* Vain.

= *Psorotheциella* Sacc. & P. Syd.

= *Stictoclypeolum* Rehm

**Asterothyrium anomalum* Kalb & Vězda

**Asterothyrium argenteum* Müll. Arg.

- **Asterothyrium aspidospermatis* (Peres) Lücking & Sérus.
 ≡ *Actinoteichus aspidospermatis* Peres
- **Asterothyrium atromarginatum* Herrera-Camp. & Lücking
- **Asterothyrium aulaxinoides* Lücking
- **Asterothyrium bisporum* L.I. Ferraro & Lücking
- **Asterothyrium chroodisciforme* Lücking
- **Asterothyrium decipiens* (Rehm) R. Sant.
 ≡ *Stictoclypeolum decipiens* Rehm
 = *Linhartia luzonica* Rehm
- **Asterothyrium filiforme* Lücking & R. Sant.
- **Asterothyrium gigantosporum* Lücking
- **Asterothyrium gyalideoides* Henssen & Lücking
- **Asterothyrium hedbergii* Kalb & Vězda
- **Asterothyrium leptosporum* Müll. Arg.
 ≡ *Asterothyrium leptospermum* Müll. Arg. [orthographic error]
- ***Asterothyrium leucophthalmum* (Müll. Arg.) R. Sant.
- ***Asterothyrium longisporum* Lücking
- ***Asterothyrium microsporum* R. Sant.
 = *Linhartia soroceae* Rehm
- **Asterothyrium monosporum* Müll. Arg.
 = *Psorotheciopsis biseptata* Rehm
 = *Psorotheciella biseptata* (Rehm) Sacc. & P. Syd.
- **Asterothyrium octomerum* R. Sant.
- **Asterothyrium pallidum* (Henssen & Lücking) L.I. Ferraro & Lücking
 ≡ *Asterothyrium anomalum* var. *pallidum* Henssen & Lücking
- **Asterothyrium pernambucense* (Cavalc.) Lücking & Sérus.
 ≡ *Actinoteichus pernambucensis* Cavalc.
- **Asterothyrium pittieri* Müll. Arg.
 ≡ *Asterothyriomyces pittieri* Cif. & Tomas.
 = *Asterothyrium elmeri* Vain.
 = *Asterothyrium robinsonii* Vain.
 = *Asterothyrium welwitschii* Vain.
 ≡ *Diplopeltopsis zimmermanniana* (Henn.) Henn. ex Höhn.
 = *Psorotheciopsis decipiens* var. *bispora* Rehm

**Asterothyrium rondoniense* Bat. & H. Maia ex Henssen & Lücking

≡ *Asterothyrium rondoniense* Bat. & H. Maia

**Asterothyrium rostratum* L.I. Ferraro & Lücking

***Asterothyrium rotuliforme* (Müll. Arg.) Sérus. & J.R. De Sloover

≡ *Gyalectidium rotuliforme* Müll. Arg.

≡ *Lopadiopsis coffeae* (Müll. Arg.) Zahlbr.

≡ *Lopadiopsidomyces coffeae* Cif. & Tomas.

≡ *Lopadiopsis floridana* Zahlbr.

**Asterothyrium segmentatum* L.I. Ferraro & Lücking

**Asterothyrium septemseptatum* Lücking

Asterothyrium septemseptatum subsp. *africanum* Lücking & Kalb

Asterothyrium septemseptatum subsp. *septemseptatum* Lücking

**Asterothyrium subargenteum* L.I. Ferraro & Lücking

**Asterothyrium tetrasporum* Lücking

**Asterothyrium umbilicatum* (Müll. Arg.) Müll. Arg.

= *Actinoteichus maranhensis* Cavalc. & Poroca

**Asterothyrium uniseptatum* Lücking

**Asterothyrium vezdae* Flakus & Lücking

Aulaxina Fée (11 species)

= *Lochomyces* Bat.

Aulaxina africana (Vain.) Zahlbr.

**Aulaxina aggregata* Lücking & Kalb

**Aulaxina dictyospora* R. Sant.

**Aulaxina epiphylla* (Zahlbr.) R. Sant.

***Aulaxina intermedia* Lücking

**Aulaxina microphana* (Vain.) R. Sant.

***Aulaxina opegraphina* Fée

***Aulaxina quadrangula* (Stirt.) R. Sant.

≡ *Lochomyces quadrangularis* (Stirt.) Bat.

= *Microxyphiomyces astrocaryifolii* Bat., J.L. Bezerra & Cavalc.

***Aulaxina submuralis* Kalb & Vězda

**Aulaxina uniseptata* R. Sant.

**Aulaxina unispora* Sérus.

Aulaxinella Xavier-Leite, M. Cáceres & Lücking (3 species)

**Aulaxinella corticola* (Kalb & Vězda) Xavier-Leite, M. Cáceres & Lücking

≡ *Aulaxina corticola* Kalb & Vězda

***Aulaxinella minuta* (R. Sant.) Xavier-Leite, Cáceres & Lücking

≡ *Aulaxina minuta* R. Sant.

= *Microxyphiomyces intermedius* Bat., J.L. Bezerra & Cavalc.

= *Microxyphiomyces minutus* Bat. & Cavalc.

**Aulaxinella multiseptata* (R. Sant.) Xavier-Leite, M. Cáceres & Lücking

≡ *Aulaxina multiseptata* R. Sant.

Basistomyces Xavier-Leite, M. Cáceres & Lücking (2 species)

***Basistomyces hyalinus* (Kalb & Vězda) Xavier-Leite, M. Cáceres & Lücking

≡ *Tricharia hyalina* Kalb & Vězda

**Basistomyces pallidus* (Vězda) Xavier-Leite, M. Cáceres & Lücking

≡ *Tricharia pallida* Vězda

Bezerroplaca Xavier-Leite, M. Cáceres & Lücking (5 species)

**Bezerroplaca fusconitida* (Lücking) Xavier-Leite, M. Cáceres & Lücking

≡ *Echinoplaca fusconitida* Lücking

**Bezerroplaca incrustatociliata* (Sérus.) Xavier-Leite, M. Cáceres & Lücking

≡ *Echinoplaca incrustaticiliata* Sérus.

***Bezerroplaca lucernifera* (Kalb & Vězda) Xavier-Leite, Cáceres & Lücking

≡ *Echinoplaca lucernifera* Kalb & Vězda

**Bezerroplaca pachyparaphysata* (R. Sant.) Xavier-Leite, M. Cáceres & Lücking

≡ *Echinoplaca pachyparaphysata* R. Sant.

**Bezerroplaca streimannii* (Sérus.) Xavier-Leite, M. Cáceres & Lücking

≡ *Echinoplaca streimannii* Sérus.

Bullatina Vězda & Poelt (1 species)

- ***Bullatina aspidota* (Vain.) Vězda & Poelt
 ≡ *Calenia aspidota* (Vain.) Vězda
 ≡ *Gyalectidium aspidotum* (Vain.) R. Sant.

Calenia Müll. Arg. (25 species)

- ≡ *Caleniomyces* Cif. & Tomas.
 = *Phlyctidium* Müll. Arg.

- **Calenia africana* Sérus.
 **Calenia areolata* Lücking
Calenia atlantica M. Cáceres & Lücking
 ***Calenia bullatinoides* Lücking
Calenia chroodisciformis Lücking
Calenia ciliata G. Thor, Lücking & Tat. Matsumoto
 ***Calenia depressa* Müll. Arg.
 = *Calenia leucothrix* Vain.
 = *Calenia meiospora* Vain.
 **Calenia dictyospora* Lücking
 **Calenia echinoplacoides* Lücking
 **Calenia flava* Lücking, Sérus. & Sipman
 **Calenia fumosa* Lücking
 ***Calenia graphidea* Vain.
 **Calenia leptocarpa* Vain.
 ***Calenia lobulata* Lücking
 ***Calenia lueckingii* C. Hartmann
 **Calenia minuta* Lücking
 **Calenia obtecta* Lücking
Calenia pernambucensis M. Cáceres & Lücking
 ***Calenia phyllogena* (Müll. Arg.) R. Sant.
 ≡ *Phlyctidium phyllogenum* Müll. Arg.
 = *Calenia graphideoides* Vain.
Calenia pseudographidea Lücking
 **Calenia rolandiana* C. Hartmann

**Calenia subdepressa* Lücking

***Calenia submuralis* Lücking

Calenia surinamensis van den Boom & Sipman

**Calenia thelotremella* Vain.

= *Calenia thelotremella* var. *lacinulata* Vain.

Caleniella Xavier-Leite, M. Cáceres & Lücking (2 species)

**Caleniella maculans* (Vain.) Xavier-Leite, M. Cáceres & Lücking

≡ *Asterothyrium maculans* Vain.

≡ *Calenia maculans* (Vain.) R. Sant.

***Caleniella triseptata* (Zahlbr.) Xavier-Leite, M. Cáceres & Lücking

≡ *Calenia triseptata* Zahlbr.

= *Calenia submaculans* R. Sant.

Caleniopsis Vězda & Poelt (2 species)

***Caleniopsis laevigata* (Müll. Arg.) Vězda & Poelt

≡ *Calenia laevigata* Müll. Arg.

**Caleniopsis tetramera* Lücking

Diploschistella Vain. (5 species)

**Diploschistella athalloides* (Nyl.) Lücking, Knudsen & Fryday

≡ *Gyalideopsis athalloides* (Nyl.) Vězda

**Diploschistella lithophila* (G. Thor & Vězda) Lücking, Sérus. & Vězda

≡ *Gyalideopsis lithophila* G. Thor & Vězda

**Diploschistella solorinelliformis* (Vězda) Lücking, Sérus. & Vězda

≡ *Gyalideopsis solorinelliformis* Vězda

**Diploschistella trapperi* (Kalb & Vězda) Lücking, Sérus. & Vězda

≡ *Gyalideopsis trapperi* Kalb & Vězda

**Diploschistella urceolata* Vain.

Echinoplaca Fée (19 species)

Echinoplaca areolata Lücking & W.R. Buck

Echinoplaca basalis W.B. Sanders & Lücking

**Echinoplaca bispora* Kalb & Vězda

***Echinoplaca campanulata* Kalb & Vězda

Echinoplaca caruaruensis M. Cáceres & Lücking

***Echinoplaca diffluens* (Müll. Arg.) R. Sant.

***Echinoplaca epiphylla* Fée

= *Spinomyces genipae* Bat. & Peres

**Echinoplaca epiphyloides* Lücking

**Echinoplaca handelii* (Zahlbr.) Lücking

**Echinoplaca hispida* Sipman

***Echinoplaca intercedens* Vězda

**Echinoplaca melanotrix* Lücking

***Echinoplaca pellicula* (Müll. Arg.) R. Sant.

= *Echinoplaca hymenula* (Müll. Arg.) R. Sant.

Echinoplaca pernambucensis Øvstedal & Elix

Echinoplaca schizidiifera J.E. Hern. & Lücking

**Echinoplaca similis* Kalb & Vězda

**Echinoplaca subsimilis* Kalb & Vězda

***Echinoplaca tetrapla* (Zahlbr.) Lücking

**Echinoplaca vezdana* Lücking & Kalb

Ferraroa Lücking, Sérus. & Vězda (1 species)

**Ferraroa hyalina* (Lücking) Lücking, Sérus. & Vězda

≡ *Gyalideopsis hyalina* Lücking

Gomphillus Nyl. (5 species)

≡ *Baeopodium* Trevis.

≡ *Microstelium* Pat.

≡ *Mycetodium* A. Massal.

**Gomphillus americanus* Essl.

***Gomphillus calycioides* (Delise ex Duby) Nyl.

≡ *Baeopodium calycioides* (Delise ex Duby) Trevis.

≡ *Mycetodium calycioides* (Delise ex Duby) A. Massal.

= *Gomphillus calycioides* f. *microcephalus* (Taylor) Nyl.

***Gomphillus hyalinus* (Pat.) Lücking, Kalb & Vězda

≡ *Microstelium hyalinum* Pat.

= *Gomphillus ophiosporus* Kalb & Vězda

Gomphillus morchelloides Lücking & Sérus.

Gomphillus pedersenii L.I. Ferraro & Lücking

Gyalectidium Müll. Arg. (47 species)

= *Gonothecium* (Vain.) Clem. & Shear

= *Tauromyces* Cavalc. & A.A. Silva

Gyalectidium appendiculatum Lücking, Lendemer & E.A. Tripp

***Gyalectidium areolatum* L.I. Ferraro & Lücking

**Gyalectidium atosquamulatum* Lücking & Kalb

**Gyalectidium aurelii* L.I. Ferraro & Lücking

**Gyalectidium australe* Lücking

**Gyalectidium barbatum* Herrera-Camp. & Lücking

***Gyalectidium catenulatum* (Cavalc. & A.A. Silva) L.I. Ferraro, Lücking & Sérus.

≡ *Tauromyces catenulatus* Cavalc. & A.A. Silva

***Gyalectidium caucasicum* (Elenkin & Woron.) Vězda

≡ *Calenia caucasica* (Elenkin & Woron.) Vězda

Gyalectidium chilense M. Cáceres & Lücking

**Gyalectidium ciliatum* Lücking, G. Thor & Tat. Matsumoto

Gyalectidium cinereodiscus Herrera-Camp. & Lücking

**Gyalectidium colchicum* Vězda

**Gyalectidium conchiferum* Lücking & V. Wirth

***Gyalectidium denticulatum* Lücking

**Gyalectidium eskucheii* Sérus. & J.R. De Sloover

**Gyalectidium fantasticum* L.I. Ferraro & Lücking

***Gyalectidium filicinum* Müll. Arg.

≡ *Gonothecium glaucovirescens* (Vain.) Clem. & Shear

**Gyalectidium flabellatum* Sérus.

- Gyalectidium floridense* Safranek & Lücking
 **Gyalectidium fuscum* Lücking & Sérus.
 **Gyalectidium gahavisukanam* Sérus.
 ***Gyalectidium imperfectum* Vězda
 **Gyalectidium kenyanum* Lücking & Kalb
 **Gyalectidium laciniatum* Lücking
Gyalectidium macaronesicum Sérus.
 **Gyalectidium maracae* Lücking
 **Gyalectidium membranaceum* Sérus. & Lücking
Gyalectidium microcarpum (Vězda) Lücking, Sérus. & Vězda
 ≡ *Bullatina microcarpa* (Vězda) Brusse
 ≡ *Calenia microcarpa* Vězda
 **Gyalectidium minus* Sérus.
Gyalectidium nashii Herrera-Camp. & Lücking
 **Gyalectidium novoguineense* Sérus.
 **Gyalectidium pallidum* Herrera-Camp. & Lücking
 **Gyalectidium palmicola* Farkas & Vězda
Gyalectidium paolae Herrera-Camp. & Lücking
Gyalectidium plicatum L.I. Ferraro & Lücking
 **Gyalectidium puntilloi* Sérus.
 **Gyalectidium radiatum* Lücking, G. Thor & Tat. Matsumoto
Gyalectidium rosae-emiliae Herrera-Camp. & Lücking
Gyalectidium sanmartinense Herrera-Camp. & Lücking
 **Gyalectidium setiferum* Vězda & Sérus.
Gyalectidium tuckerae Lücking & Lendemer
 **Gyalectidium ulloae* Herrera-Camp. & Lücking
 **Gyalectidium verruculosum* Sérus.
Gyalectidium viride Lücking, W.R. Buck & Rivas Plata
Gyalectidium xantholeucum Müll. Arg.
 **Gyalectidium yahriae* W.R. Buck & Sérus.

Gyalidea Lettau ex Vězda (43 species, plus 7 infraspecies)

- = *Actinopelte* Stizenb.
 = *Aglaothecium* Groenh.

- = *Cappellettia* Tomas. & Cif.
- = *Solorinella* Anzi
- = *Solorinellomyces* Cif. & Tomas.

Gyalidea antarctica Øvstedal & Vězda

Gyalidea asteriscus (Anzi) Aptroot & Lücking

Gyalidea asteriscus (Anzi) Aptroot & Lücking subsp. *asteriscus*

- ≡ *Solorinella asteriscus* Anzi
- ≡ *Actinopelte theobaldii* Stizenb.
- ≡ *Solorinellomyces asterisci* Cif. & Tomas.

Gyalidea asteriscus subsp. *gracilispora* Jun Yang & J.C. Wei

Gyalidea asteriscus subsp. *nigrescens* (G. Thor) Jun Yang & J.C. Wei

- ≡ *Solorinella nigrescens* G. Thor
- ≡ *Solorinella asteriscus* subsp. *nigrescens* (G. Thor) Vězda, Lumbsch & Øvstedal

Gyalidea austrocoreana S.Y. Kondr., Lőkös & Hur

Gyalidea cerina Malcolm & Vězda

Gyalidea corticola Pooja Gupta & G.P. Sinha

Gyalidea costaricensis Vězda & Hafellner

Gyalidea culbersoniana Vězda & Poelt

Gyalidea cylindrica Etayo & Vězda

Gyalidea diaphana (Nyl.) Vězda

Gyalidea dodgei Vězda

***Gyalidea fritzei* (Stein) Vězda

Gyalidea fruticola M. Svenss. & G. Thor

Gyalidea fuscoclavata M. Svenss.

Gyalidea goughensis Øvstedal

Gyalidea hensseniae Hafellner, Poelt & Vězda

***Gyalidea hyalinescens* var. *hyalinescens* (Nyl.) Vězda

Gyalidea hyalinescens var. *pauciseptata* van den Boom

Gyalidea izuensis H. Harada

Gyalidea japonica H. Harada & Vězda

Gyalidea kawanae H. Harada & Vězda

Gyalidea lecanorina (C. Knight) P. James

Gyalidea lecideopsis (A. Massal.) Lettau ex Vězda

- Gyalidea lecideopsis* (A. Massal.) Lettau ex Vězda var. *lecideopsis*
 ≡ *Cappellettia lecideopsis* (A. Massal.) Tomas. & Cif.
- Gyalidea lecideopsis* var. *convarians* (Nyl.) Vězda
- Gyalidea lecideopsis* var. *eucarpa* (Servít) Vězda
- Gyalidea lecideopsis* var. *kurdistanica* (J. Steiner) Vězda
- Gyalidea lecideopsis* var. *stigmatoides* (Nyl.) Vězda
- Gyalidea luzonensis* (Kalb & Vězda) Aptroot & Lücking
- Gyalidea madeirensis* Kalb
- Gyalidea mayaguezensis* Vězda
- Gyalidea mayaguezensis* var. *mayaguezensis* Vězda
- Gyalidea mayaguezensis* var. *antarctica* Söchting & Vězda
- Gyalidea mexicana* (B. de Lesd.) Vězda
- ≡ *Gyalidea hyalinescens* var. *mexicana* (B. de Lesd.) Vězda
- Gyalidea minuta* van den Boom & Vězda
- Gyalidea multispora* Lumbsch & Vězda
- Gyalidea novae-guineae* P. James & Vězda
- Gyalidea oosumiensis* H. Harada & A. Sakata
- Gyalidea pacifica* H. Harada & Vězda
- Gyalidea parvula* Kalb & Vězda
- Gyalidea polyspora* R. Sant.
- Gyalidea portoricensis* Vězda
- Gyalidea praetermissa* Foucard & G. Thor
- Gyalidea rivularis* (Eitner) J. Novák & Tobol.
- ≡ *Gyalidea fritzei* var. *rivularis* (Eitner) Vězda
- Gyalidea ropalosporoides* S.Y. Kondr., Lőkös & Hur
- Gyalidea roseola* (Arnold) Lettau ex Vězda
- Gyalidea saxicola* (Groenh.) Hafellner & Vězda
- ≡ *Aglaothecium saxicola* Groenh.
- Gyalidea subminuta* van den Boom
- Gyalidea subscutellaris* (Vězda) Vězda
- Gyalidea testacea* Vězda & Poelt
- Gyalidea vonkonratii* Lumbsch & Papong

Gyalideopsis Vězda (93 species, plus 2 infraspecies)

= *Epilithia* Nyl.

= *Microlychnus* A. Funk

= *Microspatha* P. Karst.

**Gyalideopsis actinoplacoides* Lücking

**Gyalideopsis aequatoriana* Kalb & Vězda

**Gyalideopsis africana* Kalb & Vězda

Gyalideopsis alnicola W.J. Noble & Vězda

Gyalideopsis altamirensis Lücking & Umaña

Gyalideopsis americana Lücking & W.R. Buck

***Gyalideopsis applanata* Herrera-Camp. & Lücking

**Gyalideopsis argentea* (Mont.) Kalb & Vězda

≡ *Echinoplaca argentea* (Mont.) R. Sant.

Gyalideopsis arvidssonii Lücking

Gyalideopsis bartramiorum Lendemer

Gyalideopsis berenice (Ellis & Everh.) Lücking & W.R. Buck

**Gyalideopsis bispora* Vězda

**Gyalideopsis brevopilosa* (Kalb & Vězda) Lücking, Sérus. & Vězda

≡ *Tricharia brevopilosa* Kalb & Vězda

≡ *Aderkomyces brevipilosus* (Kalb & Vězda) Lücking, Sérus. & Vězda

**Gyalideopsis buckii* Lücking, Sérus. & Vězda

≡ *Tricharia vezdae* W.R. Buck

**Gyalideopsis calabrica* Puntillo & Vězda

**Gyalideopsis capitata* Sérus.

Gyalideopsis chibaensis H. Harada

Gyalideopsis chicaque Moncada & Lücking

**Gyalideopsis choshuencensis* Lücking & V. Wirth

**Gyalideopsis confluens* Kalb & Vězda

Gyalideopsis crenulata Coppins & Aptroot

**Gyalideopsis cristata* (Nyl.) Lücking, Sérus. & Vězda

≡ *Epilithia cristata* Nyl.

**Gyalideopsis cyanophila* Sérus.

Gyalideopsis dominicana Vězda

Gyalideopsis ellipsoidea A.A. Menezes, M. Cáceres & Aptroot

- **Gyalideopsis epicorticis* (A. Funk) Tønsberg & Vězda
 ≡ *Microlychnus epicorticis* A. Funk
- **Gyalideopsis formosana* H. Harada & Vězda
Gyalideopsis frahmii Aptroot & Schumm
- **Gyalideopsis gigantea* Kalb & Vězda
- **Gyalideopsis giganteoides* Sérus.
- Gyalideopsis glauca* (P. Karst.) Lücking, Sérus. & Vězda
 ≡ *Microspatha glauca* P. Karst.
- Gyalideopsis globispora* Vězda
- Gyalideopsis graminicola* Vězda & Kantvilas
- **Gyalideopsis haliotidiformis* Kalb & Vězda
- Gyalideopsis halocarpa* P.M. McCarthy & Elix
- Gyalideopsis heardense* Øvstedal
- **Gyalideopsis helvetica* van den Boom & Vězda
- **Gyalideopsis intermedia* Lücking
- **Gyalideopsis japonica* H. Harada & Vězda
- **Gyalideopsis kalbii* Vězda
- **Gyalideopsis krogiae* Kalb & Vězda
- **Gyalideopsis laevithallina* Lücking
- **Gyalideopsis lambinonii* Vězda
- **Gyalideopsis lecideina* Kalb & Vězda
- **Gyalideopsis lobulata* Lücking
- Gyalideopsis lunata* H. Harada
- Gyalideopsis macarthurii* Lücking, Umaña & Aptroot
- **Gyalideopsis megalospora* Vězda & Poelt
- **Gyalideopsis mexicana* Tretiach, Giralt & Vězda
- **Gyalideopsis minima* Vězda
- **Gyalideopsis minutissima* Lücking
- **Gyalideopsis modesta* Vězda & Poelt
- **Gyalideopsis monospora* Kalb & Vězda
- **Gyalideopsis montana* Lücking
- Gyalideopsis moodyae* Lendemmer & Lücking
- **Gyalideopsis muscicola* P. James & Vězda
Gyalideopsis muscicola P. James & Vězda var. *muscicola*

- Gyalideopsis muscicola* var. *gomeræ* Etayo
- **Gyalideopsis napoensis* Kalb & Vězda
- **Gyalideopsis nepalensis* Vězda & Poelt
- **Gyalideopsis ochroleuca* Vězda
- Gyalideopsis ozarkensis* Lücking, W.R. Buck & R.C. Harris
- **Gyalideopsis pallescens* Lücking
- **Gyalideopsis pallida* Lücking
- **Gyalideopsis palmata* Kalb & Vězda
- Gyalideopsis pandani* Vězda
- **Gyalideopsis perminuta* Vězda
- **Gyalideopsis peruviana* G. Merr. ex Vězda
- **Gyalideopsis philippiae* Vězda
- **Gyalideopsis piceicola* (Nyl.) Vězda & Poelt
- Gyalideopsis pseudoactinoplaca* Lücking & Chaves
- **Gyalideopsis puertoricensis* Sipman & Lücking
- Gyalideopsis pusilla* Lücking & Tønsberg
- **Gyalideopsis robusta* Kalb & Vězda
- **Gyalideopsis rogersii* Vězda & Hafellner
- **Gyalideopsis rostrata* Kalb & Vězda
- **Gyalideopsis rubescens* Vězda
- **Gyalideopsis rubra* Lücking
- **Gyalideopsis rubrofusca* Kalb & Vězda
- Gyalideopsis saxicola* Henssen & Lumbsch
- Gyalideopsis sessile* W.B. Sanders & Lücking
- **Gyalideopsis stipitata* Kalb & Vězda
- Gyalideopsis subaequatoriana* Lücking & W.R. Buck
- Gyalideopsis submonospora* Lücking & W.R. Buck
- Gyalideopsis tuerkii* Vězda
- **Gyalideopsis vainioi* Kalb & Vězda
- Gyalideopsis vainioi* Kalb & Vězda var. *vainioi*
- Gyalideopsis vainioi* var. *semicirculata* Lücking & W.R. Buck
- **Gyalideopsis verruculosa* Vězda & Hafellner
- **Gyalideopsis vezdae* Kalb
- Gyalideopsis wesselsii* Lücking, Sipman & Chaves

**Gyalideopsis williamsii* Kalb & Vězda

**Gyalideopsis wirthii* Kalb & Vězda

Hippocrepidea Sérus. (1 species)

**Hippocrepidea nigra* Sérus.

Jamesiella Lücking, Sérus. & Vězda (4 species)

***Jamesiella anastomosans* (P. James & Vězda) Lücking, Sérus. & Vězda

≡ *Gyalideopsis anastomosans* P. James & Vězda

Jamesiella chaverriae Chaves, Umaña & Lücking

**Jamesiella perlucida* (Vězda & Hafellner) Lücking, Sérus. & Vězda

≡ *Gyalideopsis perlucida* Vězda & Hafellner

**Jamesiella scotica* (P. James) Lücking, Sérus. & Vězda

≡ *Gyalideopsis scotica* P. James

Linhartia Sacc. & P. Syd. (5 species)

**Linhartia gyalideoides* Vězda

≡ *Psorotheciopsis gyalideoides* (Vězda) Henssen & Lücking

***Linhartia patellarioides* (Rehm) Vězda

≡ *Psorotheciopsis patellarioides* (Rehm) R. Sant.

**Linhartia philippinensis* Rehm

≡ *Psorotheciopsis philippinensis* (Rehm) Lücking

**Linhartia varieseptata* Vězda

≡ *Psorotheciopsis varieseptata* (Vězda) Henssen & Lücking

Linhartia vezdana Lücking

Lithogyalideopsis Lücking, Sérus. & Vězda (4 species)

**Lithogyalideopsis aterrима* (Vězda & Poelt) Lücking, Sérus. & Vězda

≡ *Gyalideopsis aterrима* Vězda & Poelt

**Lithogyalideopsis poeltii* (Vězda) Lücking, Sérus. & Vězda

≡ *Gyalideopsis poeltii* Vězda

**Lithogyalideopsis vivantii* (Sérus.) Lücking, Sérus. & Vězda

≡ *Gyalideopsis vivantii* Sérus.

**Lithogyalideopsis zelandica* (Vězda & Malcolm) Lücking, Sérus. & Vězda

≡ *Gyalideopsis zelandica* Vězda & Malcolm

Microxyphiomyces Bat., Valle & Peres (10 species)

≡ *Setomyces* Bat. & Peres

**Microxyphiomyces cuneatus* (L.I. Ferraro & Vězda) Xavier-Leite, M. Cáceres & Lücking

≡ *Tricharia cuneata* L.I. Ferraro & Vězda

**Microxyphiomyces demoulinii* (Sérus.) Xavier-Leite, M. Cáceres & Lücking

≡ *Tricharia demoulinii* Sérus.

**Microxyphiomyces elegans* (Sérus.) Xavier-Leite, M. Cáceres & Lücking

≡ *Tricharia elegans* Sérus.

**Microxyphiomyces kashiwadanii* (G. Thor, Lücking & Tat. Matsumoto) Xavier-Leite, M. Cáceres & Lücking

≡ *Tricharia kashiwadanii* G. Thor, Lücking & Tat. Matsumoto

***Microxyphiomyces lancicarpus* (Kalb & Vězda) Xavier-Leite, M. Cáceres & Lücking

≡ *Tricharia lancicarpa* Kalb & Vězda

**Microxyphiomyces santessonianus* (Kalb & Vězda) Xavier-Leite, M. Cáceres & Lücking

≡ *Tricharia santessoniana* Kalb & Vězda

**Microxyphiomyces santessonii* (D. Hawksw.) Xavier-Leite, M. Cáceres & Lücking

≡ *Tricharia santessonii* D. Hawksw.

***Microxyphiomyces similis* (Vězda) Xavier-Leite, M. Cáceres & Lücking

≡ *Tricharia similis* Vězda

***Microxyphiomyces vainioi* (R. Sant.) Xavier-Leite, M. Cáceres & Lücking

≡ *Tricharia vainioi* R. Sant.

= *Microxyphiomyces capitulatus* Bat. & J.L. Bezerra

= *Microxyphiomyces manaosensis* Bat., Valle & Peres

= *Setomyces crescentiae* Bat. & Taltasse

= *Setomyces orchideae* Bat. & Peres

**Microxyphiomyces variratae* (Lücking & Sipman) Xavier-Leite, M. Cáceres & Lücking

≡ *Tricharia variratae* Lücking & Sipman

Microxyphiomyces sp.

Setomyces concentricus Bat., J.L. Bezerra & Cavalc.

Setomyces genipae Bat. & Peres

Setomyces giganteae Bat. & J.L. Bezerra

Setomyces minutus Bat. & H. Maia

Setomyces ocoteae Bat. & H. Maia

Setomyces orchideae Bat. & I.H. Lima

Monocalenia Xavier-Leite, M. Cáceres & Lücking (1 species)

***Monocalenia monospora* (Vězda) Xavier-Leite, M. Cáceres & Lücking

= *Calenia monospora* Vězda

≡ *Bullatina viridis* Brusse

Paragyalideopsis Etayo (4 species)

Paragyalideopsis breussii Etayo

**Paragyalideopsis floridae* (Etayo & Diederich) Etayo

≡ *Gyalideopsis floridae* Etayo & Diederich

Paragyalideopsis minuta Etayo

Paragyalideopsis stereocaulicola (Etayo) Etayo

≡ *Gyalideopsis stereocaulicola* Etayo

Paratricharia Lücking (1 species)

**Paratricharia paradoxa* (Lücking) Lücking

≡ *Tricharia paradoxa* Lücking

Phyllogyalidea Lücking & Aptroot (2 species)

Phyllogyalidea epiphylla (Vězda) Lücking & Aptroot

≡ *Gyalidea epiphylla* Vězda

Phyllogyalidea phyllophila (Vězda) Lücking & Aptroot

≡ *Gyalidea phyllophila* Vězda

Psathyromyces Bat. & Peres (2 species)

***Psathyromyces heterellus* (Stirt.) Xavier-Leite, M. Cáceres & Lücking

- ≡ *Echinoplaca heterella* (Stirt.) R. Sant.
- ≡ *Tricharia heterella* (Stirt.) Lücking
- ≡ *Aderkomyces heterellus* (Stirt.) Lücking, Sérus. & Vězda
- = *Echinoplaca affinis* Kalb & Vězda
- = *Psathyromyces rosacearum* Bat. & Peres
- = *Tricharia membranula* (Müll. Arg.) Lücking

**Psathyromyces planus* (Vězda) Xavier-Leite, M. Cáceres & Lücking

- ≡ *Aderkomyces planus* (Vězda) Lücking, Sérus. & Vězda
- ≡ *Tricharia plana* Vězda

Psathyromyces sp.

Psathyromyces minutus Bat. & J.L. Bezerra

Pseudocalenia Xavier-Leite, M. Cáceres & Lücking (1 species)

***Pseudocalenia solorinoides* (Lücking) Xavier-Leite, M. Cáceres & Lücking

- ≡ *Calenia solorinoides* Lücking

Psorotheciopsis Rehm (3 species)

- ≡ *Conicosolen* F. Schill.
- ≡ *Monospermella* Speg.

**Psorotheciopsis albomaculans* (Rehm) R. Sant.

- ≡ *Linhartia albomaculans* (Rehm) Sacc. & P. Syd.

**Psorotheciopsis guajalitensis* Lücking

Psorotheciopsis guajalitensis Lücking

***Psorotheciopsis premneella* (Müll. Arg.) R. Sant.

- = *Monospermella portoricensis* Speg.
- = *Psorotheciopsis decipiens* Rehm
- = *Psorotheciopsis decipiens* var. *decipiens* Rehm
- = *Psorotheciopsis paudalhensis* Bat. & Peres

Psorotheciopsis sp.

Conicosolen mirabilis F. Schill.

Rolueckia Papong, Thammath. & Boonpr. (3 species)

***Rolueckia aggregata* (R. Sant.) Papong, Thammath. & Boonpr.

≡ *Calenia aggregata* R. Sant.

≡ *Caleniopsis aggregata* (R. Sant.) Lücking, Sérus. & Vězda

***Rolueckia conspersa* (Stirt.) Papong, Thammath. & Boonpr.

≡ *Calenia conspersa* (Stirt.) R. Sant.

≡ *Caleniopsis conspersa* (Stirt.) Lücking, Sérus. & Vězda

= *Asterothyrium naevium* Vain.

= *Calenia lacerata* Müll. Arg.

= *Calenia pulchella* Müll. Arg.

= *Caleniomyces pulchellae* Cif. & Tomas.

Rolueckia siamensis Papong, Thammath. & Boonpr.

Roselviria Xavier-Leite, M. Cáceres & Lücking (2 species)

Roselviria lobulimarginata (Sipman & Lücking) Xavier-Leite, M. Cáceres & Lücking

≡ *Aderkomyces lobulimarginatus* Sipman & Lücking

***Roselviria purulhensis* (Lücking, Sérus. & Vězda) Xavier-Leite, Cáceres & Lücking

≡ *Aderkomyces purulhensis* (Lücking & Barillas) Lücking, Sérus. & Vězda

≡ *Tricharia purulhensis* Lücking & Barillas

Rubrotricha Lücking, Sérus. & Vězda (2 species)

**Rubrotricha helminthospora* (R. Sant.) Lücking, Sérus. & Vězda

≡ *Tricharia helminthospora* R. Sant.

***Rubrotricha subhelminthospora* Lücking

≡ *Tricharia subhelminthospora* Lücking

Serusiaxiella Xavier-Leite, Cáceres & Lücking (1 species)

***Serusiaxiella farinosa* (R. Sant.) Xavier-Leite, Cáceres & Lücking

≡ *Tricharia farinosa* R. Sant.

Sipmanidea Xavier-Leite, M. Cáceres & Lücking (1 species)

- ***Sipmanidea neotropica* (Lücking) Xavier-Leite, M. Cáceres & Lücking
 ≡ *Echinoplaca furcata* subsp. *neotropica* Lücking

Spinomyces Bat. & Peres (6 species)

- ***Spinomyces aggregatus* (Lücking) Xavier-Leite, M. Cáceres & Lücking
 ≡ *Aderkomyces albostrigosus* f. *aggregatus* Lücking
- ***Spinomyces albostrigosus* (Lücking, Sérus. & Vězda) Xavier-Leite, Cáceres & Lücking
 ≡ *Tricharia albostrigosa* R. Sant.
 ≡ *Aderkomyces albostrigosus* (R. Sant.) Lücking, Sérus. & Vězda
- **Spinomyces deslooveri* (Sérus.) Xavier-Leite, M. Cáceres & Lücking
 ≡ *Tricharia deslooveri* Sérus.
 ≡ *Aderkomyces deslooveri* (Sérus.) Lücking, Sérus. & Vězda
- **Spinomyces guatemalensis* (Lücking & Barillas) Xavier-Leite, M. Cáceres & Lücking
 ≡ *Tricharia guatemalensis* Lücking & Barillas
 ≡ *Aderkomyces guatemalensis* (Lücking & Barillas) Lücking, Sérus. & Vězda
- **Spinomyces microcarpus* (Etayo & Lücking) Xavier-Leite, M. Cáceres & Lücking
 ≡ *Tricharia microcarpa* Etayo & Lücking
 ≡ *Aderkomyces microcarpus* (Etayo & Lücking) Lücking, Sérus. & Vězda
- **Spinomyces verrucosus* (Sérus.) Xavier-Leite, M. Cáceres & Lücking
 ≡ *Aderkomyces verrucosus* (Sérus.) Lücking, Sérus. & Vězda
 ≡ *Tricharia verrucosa* Sérus.

Spinomyces sp.

Spinomyces giganteae Bat. & M.P. Herrera

Spinomyces ocoteae Bat. & H. Maia

Tricharia leucothrix Fée

Sporocybomyces H. Maia (3 species)

- **Sporocybomyces leucomuralis* (Lücking) Xavier-Leite, M. Cáceres & Lücking
 ≡ *Echinoplaca leucomuralis* Lücking

***Sporocybomyces leucotrichoides* (Vain.) Xavier-Leite, M. Cáceres & Lücking

≡ *Calenia leucotrichoides* Vain.

≡ *Echinoplaca leucotrichoides* (Vain.) R. Sant.

= *Sporocybomyces pulcher* H. Maia

**Sporocybomyces macgregorii* (Vain.) Xavier-Leite, M. Cáceres & Lücking

≡ *Echinoplaca macgregorii* (Vain.) Lücking, Sérus. & Vězda

Tricharia Fée (21 species)

***Tricharia amazonum* Vain.

= *Setomyces bellucia* Bat. & Peres

= *Tricharia macrospora* J. Hedrick

**Tricharia atrocarpa* Lücking & Sipman

**Tricharia aulaxiniformis* Lücking & Kalb

**Tricharia aulaxinoides* Kalb & Vězda

***Tricharia carnea* (Müll. Arg.) R. Sant.

Tricharia duotela W.B. Sanders & Lücking

Tricharia floridensis Lücking & W.R. Buck

***Tricharia longispora* Kalb & Vězda

Tricharia nigriuncinata Yeshitela, Eb. Fisch., Killmann & Sérus.

**Tricharia novoguineensis* Sérus.

Tricharia oaxacae Herrera-Camp. & Lücking

***Tricharia paraguayensis* (L.I. Ferraro & Lücking) Lücking

≡ *Tricharia urceolata* var. *paraguayensis* L.I. Ferraro & Lücking

**Tricharia pseudosantessonii* Lücking

Tricharia sipmanii Lücking

**Tricharia sublancicarpa* Herrera-Camp. & Lücking

**Tricharia substipitata* Vězda

Tricharia subumbrosa Lücking & W.R. Buck

**Tricharia triseptata* R. Sant.

Tricharia tuckerae Lücking & W.R. Buck

**Tricharia umbrosa* Kalb & Vězda

***Tricharia urceolata* (Müll. Arg.) R. Sant.

Tricharia sp. Lücking

Tricharia melanothrix Fée

Verruciplaca Xavier-Leite, M. Cáceres & Lücking (3 species)

***Verruciplaca calcarea* (Lücking) Xavier-Leite, M. Cáceres & Lücking

≡ *Echinoplaca verrucifera* f. *calcarea* Lücking

**Verruciplaca furcata* (Sérus.) Xavier-Leite, M. Cáceres & Lücking

≡ *Echinoplaca furcata* Sérus.

≡ *Echinoplaca furcata* subsp. *furcata* Sérus.

***Verruciplaca verrucifera* (Lücking) Xavier-Leite, Cáceres & Lücking

≡ *Echinoplaca verrucifera* Lücking

≡ *Echinoplaca verrucifera* f. *verrucifera* Lücking

Veزدamyces Xavier-Leite, M. Cáceres & Lücking (2 species)

Veزدamyces albopruinosus (Lücking) Xavier-Leite, M. Cáceres & Lücking

≡ *Gyalideopsis vulgaris* f. *albopruinosa* Lücking

***Veزدamyces vulgaris* (Müll. Arg.) Xavier-Leite, M. Cáceres & Lücking

≡ *Actinoplaca vulgaris* (Müll. Arg.) Vězda & Poelt

≡ *Gyalideopsis vulgaris* (Müll. Arg.) Lücking

≡ *Tricharia vulgaris* (Müll. Arg.) R. Sant.

Supplemental Material 4. Phylip file including the 313 taxa used in the phenotype-based phylogenetic binning approach and their scores for the 223 phenotype characters.

```

313 223
Actinoplaca_strigulacea 00010011000110000001010001010100--10001000-----
-----0100100000001111000001000-000----000000100000-010000-0100-
0100000000000000000000000000000100100-----
01000000001001100000-0010-----
Aderkomyces_albostrigosus 00010010000110000000000001000100--
0000100101000000000000----01010000000010010100011010-000----
101010000000-000000-0000-
01101111110111111001111100001000001000001100000000000-----
00000000100000-----0000-----
Aderkomyces_albostrigosus-aggregatus 00010010000110000000000001000100--
0000100100100000000000----01010000000010010100011010-000----
010110000000-000000-0000-
01101111110111111001111100001000001000001100000000000-----
00000000100000-----0000-----
Aderkomyces_carneoalbus 00010001000100000000000001100100--
0000100101000000000000----010100000000100100100000110000----
010110010100-000000-
11010011011111101111100111110000100000010000000000000000-----
----00000000100000-----0000-----
Aderkomyces_heterellus 00010010000100000000000001100100--
000010010100000001000----01000000000010011000010000-000----
100000010000-010000-
0001001100111000111111001111000000100000100000010010000001000-----
----00000000100000-----0000-----
Aderkomyces_papilliferus 000100100001000000000000101100100--
000110010100000001000----01000000000010000110010000-000----
100000011000-010000-
000110110111111011111100111100000100000100010000000000001000-----
----01000000100000-----0000-----
Aderkomyces_purulhensis 00010010000110000000000001100100--
0000100101000000000000----01000000000000010010001010-010-100010110-
00000-000000000000-
011011111101111110011111000010000001000001100000000000-----
00000000100000-----0000-----
Aderkomyces_pruinosus 00010010000100000000000001100100--
110010010100000001000----01000000000010011000010000-000----
100000010000-010000-
0001001100111000111111001111000000100000100000010010000001000-----
----00000000100000-----0000-----
Arthotheliopsis_tricharioides 00010010000100000000000001100100--
0000100101000000000000----01001000000010000110010000-000----
100000100000-010000-
010110110111110011111100011100000100000010000010000100001000-----
----00000001100010001000-0000-----
Asterothyrium_leucophthalmum 000100110000011001000000000110100--
00000110-----
010000010001000101110000000000111011010100001000000100010000000100000000
00000100110000000-----
-----1100000000
Asterothyrium_longisporum 000100110000011001000000000110100--00000110---
-----
01000001000010010100001000000111101010110101000000100010000000001000000

```

00000100111100000-----
 -----0-----
 Asterothyrium_microsporum 00010011000001100100000000010100--00000110---

 0100000100000001001000100000011111101011010100000010001000000010000000
 0000000000000000-----
 -----1110000000
 Asterothyrium_rotuliforme 000100110000011001000000000110100--00000110---

 01000001000100000010100000000101001010000000000000100010000100001111101
 11111000111100000-----
 -----1001000000
 Aulaxina_intermedia 0001001000011010000000000011001010000001000-----
 -----01000001100000110000001000-00101110000-----01100000000-
 0110111000011000010011000000101000010000000000000011100-----
 00001010100000-----0000-----
 Aulaxina_minuta 0001001000010001000000000011001010100001000-----
 -----01000001000000110000001000-00101110000-----01100000000-
 01000000000000000000000000101000010000000000000011100-----
 0000101010001000101000000-----
 Aulaxina_opegraphina 0001001100000110000000000011001010000001000-----
 -----01000001101010110000001000-00101110000-----01100000000-
 0110110000011000010011000000101000010000000000000011100-----
 0000101010001000101000000-----
 Aulaxina_quadrangula 0001001101000110000000000011001010000001000-----
 -----01000001100010110000001000-00101110000-----01100000000-
 0110010000011001000011000000101000010000000000000011100-----
 00001010100000-----0000-----
 Aulaxina_submuralis 0001001100001010000000000011001010000001000-----
 -----01000001100010110000001000-00101110000-----01100000000-
 0110011000011111100011000000101000010000000000000011100-----
 0000101010001000101000000-----
 Bullatina_aspidota 000100100000011001100000000010100--
 100011010100000010000---01000001000010010010000011000101100000-----
 -01100000000-1110111110111111001111100001000000001010000000000000000---
 -----00000000100000-----0000-----
 Calenia_bullatinoides 000100100000011101000000000110110--10001000-----
 -----01000001000000010010000010-00101100000-----01100000000-
 0110111100011111100011100000100000010000000000000001000-----
 ??????????????????????0-----
 Calenia_depressa 00010011000010000001000001010100--
 100010010100000000000---01000001010010000110010010-00101100000-----
 -0110000000110110111000011000010011100000100000010101000000000000000---
 -----00000000100000-----0000-----
 Calenia_graphidea 00010010000010000001000001010100--
 100010010100000000000---01000001010010010000000000-00101100000-----
 -01100000000-0110010000011000000011000000-----
 -----0-----
 Calenia_lobulata 00010010000001100100000000110100--10001000-----
 -----010000010000000010100010011100111100000-----
 011000001011011011111101111110011111000000-----
 -----0-----
 Calenia_lueckingii 00010011000001000001000001010100--
 100010010100000000000---01000001010010010000110000-00101100000-----
 -01100000001011101111101111100111100000100000010000000000000000000---
 -----00000000100000-----0010-----
 Calenia_monospora 00010010000001000000000001100100--
 000010010100000000000---01000001000010100010000001000100000000-----

Echinoplaca_leucotrichoides 00010010000010000001000001010100--
1000100101000000000000----01001000000010001100010000-000----
000000100000-010000-
100110110111100011110010011110000100000010000100000000001000-----
-----0000000000000100100100000-----
Echinoplaca_lucernifera 00010001000001000001000001010100--
1000100101000000000000----01001000000010000101010000-000----
000000100000-010000-
01011011001110001111100111000000100000010000000000000001000-----
-----10000000001001100000-1100-----
Echinoplaca_marginata 00010010000001000001000000110000--10001000-----
-----01001010000010000100010000-100-1000000-----000000-
01011011011111011111001111000000-----
-----0-----
Echinoplaca_pellicula 00010010000010000001000001100100--10001000-----
-----01001000000010010100000000-000----000000100000-010000-
0001001100100000100000000110000001000000001010000000000000000-----
-----00000001100000-----0000-----
Echinoplaca_tetrapla 00010001000001000001000001010100--
1000100101000000000000----01001000000010000101010000-000----
000000100000-010000-0101101100100000100000000110000000-----
-----0-----
Echinoplaca_verrucifera
000100100000100000000100000110000100110010010001000000100-----
01001000000010011000010000-000----0000001100010010010-
000100110010000011001000011000000100000000101000000000000000-----
-----00000000001001100000-0100-----
Echinoplaca_verrucifera-calcareo
00010010000010100000010000010000100110010010001000000100-----
01001000000010011000010000-000----0000001100010010010-
000100110010000011001000011000000100000000101000000000000000-----
-----00000000001001100000-0100-----
Gomphillus_calycioides 00100001101100000000000000110100--00001000-----
-----01010100000011000110010100-000----100000011000-000000-
0001101110000000111100110111100000-----
-----0-----
Gomphillus_ophiosporus 00100001101100000000000000110100--00001000-----
-----01010100000000000110010100-000----100000011000-000000-
0001101110000000111100110111111000-----
-----0-----
Gyalectidium_areolatum 00010010000010010000001001100110--10001000-----
-----010000010000000000010100000-00101000000-----
011000000010111011111011111100111100000100110-----
00000000101000--00100100110000-----0010-----
Gyalectidium_catenulatum 00010010000001010000000001100100--00001000-----
-----01000001000000000010100000-0010000101000-00000-
011000000010111011111011111100111100000100110-----
00000000101000--00100100110000-----0010-----
Gyalectidium_caucasicum 00010011010001010100000000110110--10001000-----
-----01000001000000010010000010-00101100000-----01100010000-
011011111011111100111100000100110-----00001000001000--
00100100110000-----0010-----
Gyalectidium_denticulatum 00010010000001010100000000110100--10001000---
-----00-----
-----100110-----
11001001001000--00100100110000-----0010-----
Gyalectidium_filicinum 00010011110111010101000001100100--10001100-----
-----010000010000000000000110010-0010110101010-10100-

01100010001011101111101111100111100000100110-----
00000000101000--00100100110000-----0010-----
Gyalectidium_imperfectum 00010010000010010101000001100100--10001100----
-----01000001000000000100110010-0010110101010-10100-
01100010001011101111101111100111100000110110-----
10001000001010--00100100110000-----0010-----
Gyalidea_fritzei 01000001101001001000000000110000--00000-00-----
-----01010000000010010101000000-000----010110011000-000000-
0001000000100000111010001111000000-----
-----0-----
Gyalidea_hyalinescens 01000001101001001000000000110000--00000-00-----
-----01010000000011010100000000-000----010110010100-000000-
0001000000000000100000000100000000-----
-----0-----
Gyalideopsis_applanata 000100010000100000001000001010100--10001000-----
-----010000000000010000110010000-000----101000011000-000010-
0101101101100000110000000110000001000000100000000000000000001000-----
-----00000000100000-----0000-----
Gyalideopsis_epithallina 10011010000110-----0-----
-----010100000000000010010000000-000----101010000000-001000-
0001001100000000000000000000000000001000000101000110000000011100-----
-----?????????????????????????0-----
Gyalideopsis_vulgaris 00010011000110010001000001100100--10001000-----
-----01000000000010010000110000-000----010110000000-001100-0000-
11101111101111110011110000010000001000010000000000000010-----
01000000100000-----0000-----
Gyalideopsis_vulgaris-albomarginata 00010011000010010001000001100100--
10001000-----01000000000010010000110000-000----
0101100100010001100-0000-
1110111110111111001111000001000000100001000000000000010-----
01000000100000-----0000-----
Jamesiella_anastomosans 00100001000010001000000001100100--00001000-----
-----01010000010010001100010000-000----101011010100-000010-
100110110010000011001000111000000100101-----
---00-----10-----
Linhartia_patellarioides 000100110000011001000000000101010100000110----
-----010100010000000100100010000000----
101000010110000001101000000010000000000000000000000000000000000-----
-----0-----
Psorotheciopsis_premneella 000100110000011001000000000010100--00000110--
-----010100010000100000010100000000----
101000000110000001101001100001111110000000000111100110-----
-----0-----
Rolueckia_aggregata 000100100001000000000000110101010110001000-----
-----01000001000100110000000010-00101100000-----01100000000-
01000000000100000000100000000-----
-----0-----
Rolueckia_conspersa
000100100001000010000000110101010110001001?????????????----
01000001000000110000000010-00101100000-----01100000000-
0100000000000000000000000000000-----
-----0-----
Rubrotricha_subhelminthospora 00010010000100000000000001100100--
0000100101001000000001101001010000000000010100001010-000----
101010000000-000000-0000-
011001000001110001001110000010000000001000000000000010000-----
01000000100000-----0000-----

Tricharia_amazonum 00010010000010000001000001010100--
100010011100011001000----01010000000010011000010010-000----
101010000000-001100-0000-
011011111011111100111110000100000010000000000000011100-----
00000000100000-----0000-----
Tricharia_carnea 00010010000010000001000001010100--
1000100111000110010010101010100000000100101000000110000----
101010010100-001100-
1001001101111101111100111110000100000010000000000000011100-----
----00000000100000-----0000-----
Tricharia_farinosa
0001001110010000000100000110010101100010011100011001000----
0101000000000000001000100011000----1010100000011001011-
0001101101111101111100111110000100000010000000000000011100-----
----00000000100000-----0000-----
Tricharia_hyalina 000100100001000000000000000100100--
000010011100011010000----011100000000000110000001010-000----
101010000000-001100-0100-
011001110001111110011110000100000010000000000000011100-----
00000000100000-----0000-----
Tricharia_lancicarpa 000100100001000100000000001100100--
000010011100011000000----01000000000010010100000010-010-100101010-
00000-00100000000-
011011111011111100111100000100000010000000000000011100-----
00000010100000-----0000-----
Tricharia_longispora 00010010000010000001000001010100--
100010011100011001001010001110000010010000110010010-000----
010110010000-001100-
00011011011111101111100111110000100000010000000000000011100-----
----0000000110001000001000000-----
Tricharia_paraguayensis 00010010000100000001000001010100--
100010011100011001000----01010000000010010100010010-000----
010110000000-001110-
01011011011111101111100111110000100000010000000000000011100-----
----00000000100000-----0000-----
Tricharia_similis 00010010000100010000000001100100--
000010011100011000000----01110000000010010100000010-000----
101010010100-000000-1000-01100110000110010001110000000-----
-----0-----
Tricharia_urceolata 00010010000010000001000001010100--
100010011100011001000----01010000000000010100010010-000----
101010011000-001110-
00011011011111101111100111110000100000010000000000000011100-----
----00000000100000-----0000-----
Tricharia_vainioi 00010010000110010000000001100100--
000010011100011000000----01000000000000010100000000-000----
101000010100-001010-
00010011011111101111100111100000100000010000000000000011100-----
----0000000110001000001000000-----
Aderkomyces_armatus 00010001000010000000000000110100--
100010010100000000100----01000000000010000110000000-000----
101000011000-000000-
00010011011111101111100111100000100000010101000000000000000-----
----00000000100000-----0000-----
Aderkomyces_couepiae 00010010000100000000000001100100--
000010010100000000000----01000000000010000110010000-000----
100000011000-010000-

```

00011011011111101111100111100000100000010000010000100001000-----
-----00000000100000-----0000-----
Aderkomyces_cretaceus 00100001100010000000100000010000--
100010010100000000010----010000000100100010000100010000----
101010000000-000000-
11011011????????????????????????0010000000001000000000000000-----
-----01000000100000-----0000-----
Aderkomyces_cubanus 00010010000100000000000001100100--
0000100101000000000000----010100000000000001100010000-000----
101010010100-001010-0101101100000000100000000100000000-----
-----0-----
Aderkomyces_deslooveri 000100100000100100000000000110100--
0000100101000000000000----010100000000000000101010000-000----
101010010100-000011-
01111011011111101111100111110000100000010000011000000001000-----
-----00000000100000-----0000-----
Aderkomyces_dilatatus 000100100001000000000000101100100--
000110010100000001000----01000000000010000110010000-000----
100000011000-010000-
00011011011111101111100111100000100000010000010000100001000-----
-----00000000100000-----0000-----
Aderkomyces_fumosus 001000100000100000000000000110100--
000010010100100001000----010100000000010000011010000-000----
101010000000-000010-
110110110000000011001000111000000100000000000010000100001000-----
-----00000000100000-----0000-----
Aderkomyces_guatemalensis 00010010000100000000000001100100--
0000100101000000000000----010100000000000001100010000-000----
101000010100-001010-
00011011001111001111100011100000100000010000011000000001000-----
-----?????????????????????????0-----
Aderkomyces_lobulicarpus
0001000100001000010000000011010100100010010100000000000----
01010000000010000100010000-000----010110010010-001011-
011110110111110011111001111100001000000101010000000000001000-----
-----0000000110000000001000000-----
Aderkomyces_microcarpus 000100100001100000000000000100100--
000010010100000010000----01000000000000000010010000-000----
101000011000-001000-
00000011001110001111100011110000100000010000011000000001000-----
-----?????????????????????????0-----
Aderkomyces_microtrichus 00010010000010000001000000110100--
100010010100000010000----01000000000010001100010000-000----
100000000000-000000-
01010011000000000000000000001000000100000000000000001000-----
-----?????????????????????????0-----
Aderkomyces_planus 000100100001000000000000001100100--
000010010100000001000----01000000000010001100010000-000----
101000010000-010000-00010011001110001111100111000000-----
-----0-----
Aderkomyces_ramiferus 00100001000010001000000001100100--
100010010100000001100----01000000010111000101010000-000----
101010011000-000000-
10011011000000001111100111000000100000010000011000000001000-----
-----?????????????????????????0-----
Aderkomyces_subalbostrigosus 00010001000100010000100001100100--
1000100101000000000000----01010000000010010010010000-000----
101010011000-000000-

```

```

01010011001100001111110011100000010000001000000000000001000-----
-----????????????????????????????0-----
Aderkomyces_subplanus 001000100000100000000000000110100--
0000100101000000000000-----01000000010010000101010000-000-----
101000000000-000010-0111101101111100111110011111000000-----
-----0-----
Aderkomyces_verruciferus 00010001000010000000100001010100--
1000100101000000000000-----01000000000010001100010000-000-----
100000000000-000000-
01010011011111101111100111100000100000010000011000000001000-----
-----????????????????????????????0-----
Aderkomyces_verrucosus 00010010000100000000100001100100--
1000100101000000000000-----01010000000010011000000010-000-----
101010000000-000000-0000-0110111111011111001111100000-----
-----0-----
Arthotheliopsis_hymenocarpoides 00010010000001000000000001100100--
0000100101000000000000-----01001000000010000110010000-000-----
100000100000-010000-
010110110010000011001000011000000100000010000000000000001000-----
-----00000001100010001000-0000-----
Arthotheliopsis_planicarpus 0001001000010000000000000001100100--
0000100101000000001000-----01000000000010000110010000-000-----
100000011000-000000-
000100110011100011111100011100000100000010000010000100001000-----
-----00000001100010001000-0000-----
Arthotheliopsis_serusiauxii 0001000100001000000000000001100100--
0000100101000000000000-----01001000000010000101010000-000-----
100000100000-010000-
010110110010000011001000010000000100000010000010100000011100-----
-----00000001100000001000-0000-----
Asterothyrium_anomalum 00010011000001100100000000010100--00000110-----
-----
01000001000110001110010000000111111010110001000000100010000000011111100
11111001111100010-----
-----0-----
Asterothyrium_argenteum 000100110000011001000000000110100--00000110-----
-----
0100000100001000011001000000011110101011000100000010001000000010000000
00000100111000000-----
-----1001011110
Asterothyrium_aspidospermatis 00010011000001100100000000010100--
00000110-----00-----
-----0-----
-----1000100100
Asterothyrium_atromarginatum
000100110000011001000000000101010100000110-----
0100000100000001001000100000011111101011010100000010001000000010000000
0000000000000000-----
-----1110000000
Asterothyrium_aulaxinoides 00010011000001100100000000010100--00000110--
-----
01000001000010010010001000000111111010110101000000100010000000011111000
00000001111000010-----
-----0-----
Asterothyrium_bisporum 00010011000001100100000000010100--00000110-----
-----
01000001000010000101010000000111111010110001000000100010000000001111001

```

```

11111000111100010-----
-----0-----
Asterothyrium_chroodisciforme 00010011000001100100000000010100--
00000110-----
0100000100001100010101000000011110101011000100000000010000000011111000
00000001111100010-----
-----0-----
Asterothyrium_decipiens 00010011000001100100000000010100--00000110-----
-----
01000001000010010010001000000111111010110101000000100010000000010000000
00000000111100010-----
-----1110000000
Asterothyrium_filiforme 000100110000011001000000000110100--00000110-----
-----00-----
-----0-----
-----1000111111
Asterothyrium_gigantosporum 00010011000001100100000000010100--00000110-
-----
01000001000010010100001000000111101010110101000000100010000000001110000
00000000111100010-----
-----0-----
Asterothyrium_gyalideoides 00010011000001100100000000010100--00000110--
-----
0100000100001001000000100000000000100000000000000100010000000100000000
00000000100000000-----
-----1100000000
Asterothyrium_hedbergii 00010011000001100100000000010100--00000110-----
-----
01000001000010010010001000000111111010110101000000100010000000011100000
00000000110000010-----
-----1110000000
Asterothyrium_leptosporum 00010011000001100100000000010100--00000110---
-----
01000001000100010010000000000111011010100001000000100010000000100000000
00000110110000000-----
-----1001000000
Asterothyrium_monosporum 00010011000001100100000000010100--00000110----
-----
01000001000010001100010000000111101010110001000000100010000000011111101
00000001111100010-----
-----0-----
Asterothyrium_octomerum 00010011000001100100000000010100--00000110-----
-----
01000001000010010110000000000111011010100001000000100010000000101110001
10000100111100000-----
-----0-----
Asterothyrium_pallidum 00010011000001100100000000010100--00000110-----
-----
01000001000010001110010000000111101010110001000000100010000000011111100
11111001111100010-----
-----0-----
Asterothyrium_pernambucense 000100110000011001000000000110100--00000110-
-----00-----
-----0-----
-----1000100000
Asterothyrium_pittieri 00010011000001100100000000010100--00000110-----
-----
01000001000010000101010000000111111010110001000000100010000000011111000

```



```

00000001111100010-----
-----0-----
Asterothyrium_rondoniense 00010011000001100100000000010100--00000110---
-----
0100000100001000110001000000011110101011000100000000010000000011111000
00000001111100010-----
-----0-----
Asterothyrium_rostratum 00010011000001100100000000010100--00000110-----
-----00-----
-----0-----
-----1111000000
Asterothyrium_segmentatum 00010011000001100100000000010100--00000110---
-----
01000001000000010110000000000111011010100001000000100010000000101000001
10000100110000000-----
-----0-----
Asterothyrium_septemseptatum 00010011000001100100000000010100--
00000110-----
0100000100010000001000100000011110101011000000000010001000000000000001
10000000110000000-----
-----1001000000
Asterothyrium_subargenteum 000100110000011001000000000110100--00000110--
-----
01000001000000010010001000000111111010110101000000100010000000100000000
00000000000000000-----
-----1001010100
Asterothyrium_tetrasporum 00010011000001100100000000010100--00000110---
-----
01000001000010000101010000000111111010110001000000100010000000001110000
00000001111100010-----
-----0-----
Asterothyrium_umbilicatum 00010011000001100100000000010100--00000110---
-----00-----
-----0-----
-----1000110110
Asterothyrium_uniseptatum 00010011000001100100000000010100--00000110---
-----
01000001000010001100010000000111101010110001000000100010000000011111100
00000001111100010-----
-----0-----
Asterothyrium_vezdae 00010011000001100100000000010100--00000110-----
-----
01000001000010010100010000000111111010110101000000100010000000011110001
11000100111100000-----
-----1110000000
Aulaxina_aggregata 10011010000010-----
-----01000001101100010110001000-00101110000-----01100000000-
011000000000000000000000000000000-----
-----0-----
Aulaxina_corticola 00100010000100000000000000011001010100001000-----
-----01000001100000110000001000-00101110000-----01100000000-
011011100001100001001100000010100001000000000000000011100-----
0000101010001000101000000-----
Aulaxina_dictyospora 000100100000101000000000011001010000001000-----
-----01000001100010110000001000-00101110000-----01100000000-
01101111101111110011110000010100001000000000000000011100-----
0000101010001000101000000-----

```



```

0110000000000000000000100000000-----
-----0-----
Calenia_microcarpa 00010010000010010000100001010100--
100010010100000010000-----
0100000100000011000000001100010100101010000000-01100010000-
11101111110111111001111000000-----
-----0-----
Calenia_minuta 00010010000100010001000001100100--10001000-----
---01000001000000010100010010-00001100000-----
01100000101001101100000110000000110000000-----
-----0-----
Calenia_obtecta 00010010000010000001000001000100--
1000100101000000000000-----01000001000010010100010001000111100000-----
-01100000101101101110000111000100111000000-----
-----0-----
Calenia_philippinensis 00010010000010000000100001100100--10001000-----
-----01000001000010010100010000-00101100000-----
0110000010110110111100011111000111000000-----
-----0-----
Calenia_pruinosa 00010010000010000001000001010100--10001000-----
-----01000001000010010100010001000101100000-----
011000001011011011111011111001111100000-----
-----0-----
Calenia_rionigrensis 00010010000100000000001001001100--10001000-----
-----01000001000010010010000010-00111000000-----01100000000-
01100100000110010000100000000-----
-----0-----
Calenia_rolandiana 00010010000100000001000001010100--10001000-----
-----01000001000000110000000010-00101100000-----01100000000-
0110111111011111100111110000110000010000000000000011100-----
00000000100000-----0000-----
Calenia_subdepressa 00010011000100000001000000110100--
1000100101000000000000-----01000001000010000110010010-00101100000-----
-01100000101101101100000100000000100000000-----
-----0-----
Calenia_thelotremella 00010010000010000001000001010100--
1000100101000000000000-----01000001000000010010000010-00101100000-----
-01100000000-01101111000111000100111000000-----
-----0-----
Calenia_viridis 00010010000001000000000001100100--
0000100101000000000000-----01000001000010100010000001000100000000-----
-01100000001011101111101111100111110000100000010000000000000000000-----
-----00000000100000-----0010-----
Caleniopsis_tetramera 000100100001000100000000101101010010001000-----
-----01000001000000010010000010-00101100000-----00001000000-
01100000000100000000100000001010000100000000000000011000-----
????????????????????????????0-----
Diploschistella_athaloides 01000001101001000000000000110100--00001000-
-----01000001010011000001010000-100-110101010-10010-
00001110111101100110000110010001110000000-----
-----0-----
Diploschistella_lithophila 01000001110001001000000000110000--00001000--
-----01000001010010000100010000-100-100101010000000-
0000110010110110010000011001000110000000100000011000010100000001000-----
-----????????????????????????0-----
Diploschistella_solorinellaeformis 01000001101001000000000000110000--
00001000-----01000001000011000001010010-100-100010110-

```

```

10010-00001111101101100100000110010001110000000-----
-----0-----
Diploschistella_trapperi 010000010000010000000000000010000--00001000----
-----010000010000110001010100010100-000101000-10100-
00001100101001100000000110010000110000000-----
-----0-----
Diploschistella_urceolata 010000000100110000000000000110100--00001000---
-----01000001010011000001010000-100-110101010-10010-
00001110111101100110000110010001110000000-----
-----0-----
Echinoplaca_amapensis 0001001000001010000000000000100010010001000-----
-----010010100000100001100100010000----000000100000-010010-
0001101101100000100000000100000000-----
-----0-----
Echinoplaca_atrofusca 0001001110000110000000000000100010010101000-----
-----01001010000010000101010000-000----0000000100010010000-
010110110011000011001000110000000101000010000000000000011100-----
-----?????????????????????????????0-----
Echinoplaca_atromuralis 0001001100000110000000000000100010010101000-----
-----01001010000010000101010000-000----0000000100010010000-
0101101101111101111100111100000101000010000000000000011100-----
-----?????????????????????????????0-----
Echinoplaca_bispora 00100010000010000001000001010100--
100010010100000010000----01001000010010000100010000-000----
000000100000-010000-
010110110111110011111100011110000100000010000000000000001000-----
-----0000000010001000100000000-----
Echinoplaca_epiphylloides 00010010000010000001000001010100--
1000100101000000001000----01001000000010010100000000-000----
000000100000-010000-
000100110010000011000000011000000100000010101000000000000000-----
-----?????????????????????????????0-----
Echinoplaca_furcata
00010010000010000000010000110000100110010010001000000100----
010010000000100110000100010000----0000001100010010010-
000100110111111011111100111100000100000000101000000000000000-----
-----00000000001001100000-0100-----
Echinoplaca_fusconitida 00010001000001000001000001010100--
1000100101000000000000----01001000000010000101010000-000----
000000100000-010000-
010110110111111011111100111110000100000010000000000000001000-----
-----00000000001001100000-0100-----
Echinoplaca_gemmifera 00010010000010000001000001100100--10001000-----
-----01001000000010010100000000-000----000000100000-010000-
000100110010000010000000011000000100100-----
-----00010000001001100000-0010-----
Echinoplaca_handelii 00010010000010000001000001100100--
100010010100000001000----01001000000010010100010000-000----
000000100000-010000-
010100110010000011001000011000000100000010101000000000000000-----
-----00000000100000-----0000-----
Echinoplaca_hispida 00010010000010000001000001010100--
1000100101000000000000----01001000000010011000000000-000----
000000100000-010000-
000100110010000011000000011000000100000010101000000000000000-----
-----00000000100000-----0000-----
Echinoplaca_incrustatociliata 00010001000010000001000000110100--
100010010100001100000----01001000000000001100000000-000----

```

```

000000100000-010010-
000100110111111011111100111110000100000010000100000000001000-----
-----00000000100001100000000000-----
Echinoplaca_leucomuralis 00010010000010000001000001010100--
1000100101000000000000----01001000000010001100010000-000----
000000100000-010000-
100110110111111011111100111100000100000010000100000000001000-----
-----00000000000000100100100000-----
Echinoplaca_macgregorii 00010010000010000001000001010100--
1000100101000000000000----01001000000010001100010000-000----
000000100000-010000-1001101100100000100000000100000000-----
-----0-----
Echinoplaca_madagascariensis 00010010000010000000000001100100--
1000100101000000000000----01001000000010010100010000-000----
000000100000-010000-000110110000000000000000000000000000-----
-----0-----
Echinoplaca_melanothrix 00010010000010000001000001010100--10001000-----
-----01001000000010010100000000-000----000000100000-010000-0100-
011011111001111110011110000011000001000000000000000011100-----
????????????????????????????0-----
Echinoplaca_pachyparaphysata 00010001000001000001000001010100--
1000100101000000000000----01001000000010000101010000-000----
000000100000-010000-
010110110011100011111100111100000010000001000000000000001000-----
-----????????????????????????????0-----
Echinoplaca_purpurea 00010010000010000001000001010100--10001000-----
-----010010000000100001100100010000----000000100000-010000-
0101101101111110111111001111100000-----
-----0-----
Echinoplaca_similis 00100010000010001001000000110000--
1000100101000000000000----01001000000011000100010000-000----
000000100000-010000-
0101101101111110111111001111100001000000101010000000000001000-----
-----00000000100000-----0000-----
Echinoplaca_streimannii 00010001000010000001000001010100--
1000100101000000000000----01001000000010000101010000-000----
000000100000-010010-
0101101101100000111111001111000001000000100000000000000001000-----
-----00000000001001100000-0100-----
Echinoplaca_subsimilis 00100010000010001001000000110000--
1000100101000000000000----01001000000011000100000000-000----
000000100000-010000-
0101101101111110111111001111100001000000100000000000000001000-----
-----00000000100000-----0000-----
Echinoplaca_triseptata 0001001100000110000000000001100010010101000-----
-----010010100000100001100100010000----0000001100010010000-
0101101100100000100000001100000001000000100000000000000001000-----
-----????????????????????????????0-----
Echinoplaca_vezdana 00010010000010001000100001100100--10001000-----
-----01001000010011010100010000-000----000000100000-010000-
0001101101111000111111000111000000-----
-----0-----
Echinoplaca_wilsonii 0001001100000110000000000000100010010101000-----
-----01001010000010000101010000-000----0000000100010010000-
010110110011000011000010011000000101000010000000000000000011100-----
-----????????????????????????????0-----
Epilithia_cristata 010000?????????000000000000100000--00001000-----
-----00-----

```



```

-----10000000000010000100011100-----
00000000000100-----0000-----
Gomphillus_americanus 00100001101010000000000000110100--00001000-----
-----0101010000000000110010100-000----100000011000-000000-
00011011100000001111001101111000010000010000001000000101000-----
-----00001000000100-----0000-----
Gyalectidium_atrosquamulatum 00010001000010010101000001010100--
10001100-----01000001000000000100110010-0010110101010-
10100-01100010001011101111101111100111100000110110-----
--00000000001001--00100100110000-----0010-----
Gyalectidium_aurelii 00010010000010010001000001100100--10001100-----
-----00-----
-----110110-----00110000010101--
00100100110000-----0010-----
Gyalectidium_australe 00010010000010110100000000110100--10001000-----
-----01000001000000010010000010-00101100000-----01100010000-
0110111111011111100111100000110110-----00001000000100--
00100100110000-----0010-----
Gyalectidium_barbatum 00010010000001010100000000110100--10001000-----
-----00-----
-----110110-----00100000010110--
00100100110000-----0010-----
Gyalectidium_ciliatum 00010011010111010100000000110110--10001000-----
-----01000001010000010100000010-00101100000-----01101011000-
0110111111011111100111100000110110-----10001101001000--
00100100110000-----0010-----
Gyalectidium_colchicum 00010000000010010101000001100100--10001100-----
-----00-----
-----100110-----00001000001000--
00100100110000-----0010-----
Gyalectidium_conchiferum 00010001000010010000000001100100--00001000----
-----00-----
-----110110-----00100000000000--
-00100100110000-----0010-----
Gyalectidium_corticola 00100010000010001001000001100100--10001000-----
-----01000001010100000001010001000101100000-----
01100000101111101111100111111001111100000-----
-----0-----
Gyalectidium_eskucheii 00010011010010010101000001100100--10001100-----
-----01000001000000000100100010-0010110101010-10100-
01100010001011101111101111100111100000100110-----
01001101000000--00100100110000-----0010-----
Gyalectidium_fantasticum 00010001000010010000001001100110--10001000----
-----00-----
-----110110-----00110000000101-
-00100100110000-----0010-----
Gyalectidium_filicinum-lobatum 00010010000010010101000001100100--
10001100-----01000001001000000000110010-0010110101010-
10100-01100010001011101111101111100111100000100110-----
--00000000101000--00100100110000-----0010-----
Gyalectidium_flabellatum 00010010000010110100000000110100--10001000----
-----01000001000000010010000010-00101100000-----
01100010000-011011111011111100111100000110110-----
00100000000100--00100100110000-----0010-----
Gyalectidium_fuscum 00010001000010010101000001100100--10001100-----
-----01000001000000000100110010-0010110101010-10100-
01100010001011101111101111100111100000100110-----
00001000101000--00100100110000-----0010-----

```

Gyalectidium_gahavisukanum 00010010000010010100000000110110--10001000--
 -----01000001000000010010000010-00101100000-----
 01100010000-0110111111011111100111100000110110-----
 00001000000100--00100100110000-----0010-----
 Gyalectidium_kenyanum 00010001000010010100000000110100--10001000-----
 -----01000001000000010010000010-00101100000-----01100010000-
 0110111111011111100111100000100110-----11001001000000--
 00100100110000-----0010-----
 Gyalectidium_laciniatum 00010010000001010001000001100100--10001000-----
 -----00-----
 -----100110-----01000000010000--
 00100100110000-----0010-----
 Gyalectidium_maracae 00010010000010010100000000110100--10001000-----
 -----00-----
 -----110110-----00001001000100--
 00100100110000-----0010-----
 Gyalectidium_membranaceum 00010001000010010100000001010010--10001000---
 -----00-----
 -----110110-----
 10000000001010--00100100110000-----0010-----
 Gyalectidium_minus 00010010000001010100000000110100--10001000-----
 -----01000001000000010010000010-00101100000-----01100010000-
 0110111111011111100111100000110110-----00000001000110--
 00100100110000-----0010-----
 Gyalectidium_novoguineense 00010010000010110100000000110100--10001000--
 -----01000001000000010010000010-00101100000-----
 01100010000-0110111111011111100111100000110110-----
 00001001000100--00100100110000-----0010-----
 Gyalectidium_pallidum 00010010000011000001000001100100--10001000-----
 -----00-----
 -----100110-----10001001000110--
 00100100110000-----0010-----
 Gyalectidium_palmicola 00010010000010010000001001100110--10001000-----
 -----010000010000000100010000010-00101100000-----
 011000100010111011111011111100111100000110110-----
 00100000010100--00100100110000-----0010-----
 Gyalectidium_puntilloi 00010001010010010000001001100110--10001000-----
 -----00-----
 -----110110-----00000000011000--
 00100100110000-----0010-----
 Gyalectidium_radiatum 00010010000010010101010001100100--10001000-----
 -----010000010000000000000110010-0010110101010-10100-
 0110001000101110111111011111100111100000100110-----
 00001001001000--00100100110000-----0010-----
 Gyalectidium_setiferum 00010000000010010001000001100100--10001000-----
 -----00-----
 -----100110-----01001101000000--
 0010010011001000001000010-----
 Gyalectidium_ulloae 00010010000001110100000000110100--10001000-----
 -----00-----
 -----110110-----10001001000101--
 00100100110000-----0010-----
 Gyalectidium_verruculosum 00010010000010010101000001100100--10001000---
 -----010000010000000000000110010-0010110101010-10100-
 0110001000101110111111011111100111100000100110-----
 00001001001000--00100100110000-----0010-----
 Gyalectidium_yahriae 001000100000100100000000011001011000001000-----
 -----00-----

-----100110-----01000000100000--
00001100100001000100-0010-----
Gyalideopsis_actinoplacoides 00010001000010000001000001010100--
10001000-----01000000000010000110010000-000----
101000011000-000010-
0101101101111110111110011111000010000001000000000000011100-----
-----00000000100000-----0000-----
Gyalideopsis_aequatoriana 00100001000010000001000000010100--10001000---
-----01000000010010000100000000-000----010100011000-000000-
0000-01100111100111111001111000000100000011000010001000001000-----
-----00000000100000-----0000-----
Gyalideopsis_africana 001000011001000000000000000110100--00001000-----
-----01010000000011000100010000-000----101010010100-000010-
0001101100111110011111100111100000100000100010000000000011000-----
-----01000000000100-----0000-----
Gyalideopsis_albopruinosa 0001000100001010000001000011001010010001000---
-----010100000000100011000100010000----010110010100-001010-
0101001101111110111111001111100001000000100001000000000001000-----
-----?????????????????????????????????0-----
Gyalideopsis_argentea 001000100000100000000000000110000--00001000-----
-----01000000000010000101010000-000----101000011000-000000-
01011011011111101111100111100000100000010000010000100011100-----
-----?????????????????????????????????0-----
Gyalideopsis_bispora 000100010000101000000000001010100--10001000-----
-----01010000000010010100010000-000----101011011000-000010-
00010011011111100111111001111000000-----
-----0-----
Gyalideopsis_brevipilosa 001000100000100000000000000110100--00001000----
-----01000000010011000101010000-000----101000011000-000000-
0001101101111110111111001111000001000000100000000000000000000-----
-----?????????????????????????????????0-----
Gyalideopsis_buckei 001000000000100010000000000110100--00001000-----
-----01000000000010000101010000-000----101000011000-000010-
10011011001110001111110011110000001000000000000011000000011100-----
-----00000000000100-----0000-----
Gyalideopsis_bullata 00010001000010110100000000010100--10001000-----
-----010000000000000000101010000-000----101010000000-001011-
0101101100000000100000000100000001100000100000000000000001000-----
-----?????????????????????????????????0-----
Gyalideopsis_calabrica 001000000000100000000000000100000--00001000-----
-----00-----
-----10000001100001000010000100011100-----
00000000000100-----0000-----
Gyalideopsis_capitata 0010000100010000000000000001100100--10001000-----
-----01010000000000010100010010-000----101010010100-000010-
0001001101111110111111001111100001000000100100000000000000000-----
-----01000000110000-----0000-----
Gyalideopsis_choshuencensis 00010001000010000000100001100100--10001000-
-----01000000000010010100010000-000----101000011000-000010-
01010011011100001111110011110000010000001000000000000000011100-----
-----00000000100010---01000000-----
Gyalideopsis_cochlearifera 10011010000110-----0-----
-----010100000000000000101010000-000----101011010010-001011-
011110110000000000000000000000000000000100000010000010100000011100-----
-----00000000000100-----0000-----
Gyalideopsis_confluens 0010001000001000000000000000110100--00001000-----
-----01000000010110010100010000-000----101010011000-000010-

```

010100110011100011111100111100000100000011000010000100011100-----
-----00000000100000-----0000-----
Gyalideopsis_cyanophila 001000011000100000000000001100100--00001000-----
-----00-----
-----10000010000000000000000011000-----
00000000000100-----0000-----
Gyalideopsis_floridae 00100100010010110000000001100000--00000000-----
-----01010000000010000101010000-000----010111000000-000011-
0101101100000001000000001000000000-----
-----0-----
Gyalideopsis_formosana 01000010000010001000000001100000--00001000-----
-----01010000010110000100000000-000----010110010100-000010-
0001001100100000110010001110000000-----
-----0-----
Gyalideopsis_gigantea 00100001000010001000000000010100--00001000-----
-----01010000000010000101010010-000----101010010010-000011-
01011011011111101111100111110000100000100000010010000001101-----
-----00001000110000-----0000-----
Gyalideopsis_giganteoides 00100010000100000000000001100100--00001000-----
-----00-----
-----100000100000010010000001101-----
--0000100010000100100110000-----
Gyalideopsis_haliotidiformis 00100010000010001000000000110100--
00001000-----00-----
-----100000001000010001000011100-----
-----00000000110000-----0000-----
Gyalideopsis_helvetic 00100000001100000000000001100100--00001000-----
-----11010000000110001100010100-000----011000011000-000010-
0101101100101000110010000110000000-----
-----0-----
Gyalideopsis_hyalina 00010001000010000000000001100100--00001000-----
-----01010000000000110000000000-000----101010000000-001100-0100-
0110110000011001000111000000100110-----00000010000100--
00000000000100-----0000-----
Gyalideopsis_intermedia 000100010000100000000100001100100--10001000-----
-----01010000000010010010000000-000----010110000000-000000-
010100110111111011111001111000001000000100000000000000000-----
-----00000000100000-----0000-----
Gyalideopsis_japonica 00100010000010000000000001100100--00001000-----
-----01000000010010000110000000-000----101000011000-000000-
0001001101111110111110011110000010000000100001000000011100-----
-----00001000000000-----0000-----
Gyalideopsis_kalbiai 00100010000010000000000000110100--00001000-----
-----011100000100101100000000010000----1010100100010000000-
00010011001000001100100011000000010000000001000000000011000-----
-----0100000000010100101000000-----
Gyalideopsis_krogiae 00100010000010000000000000110100--00001000-----
-----01000000000100000110100010000----101010010010-000011-
01111011011111101111100111100000100110001000010000000011000-----
-----00001000100000-----0000-----
Gyalideopsis_laevithallina 000100010001000000000000011001010000001000--
-----01010000000010010100000000-000----010110010000-000010-
010100110111111011111001111000001010000100000000000000000-----
-----?????????????????????????????0-----
Gyalideopsis_lambinonii 00100010000010000000000000110100--00001000-----
-----01000000010011000101010000-000----101000011000-000000-
000110111111011111100111110000100000001000010000000111100-----
-----00001000100000-----0000-----

```

Gyalideopsis_lectideina 010000100000010000000000001100100--00001000-----
 -----01010000000010000001010000-000----101010010010-000011-
 0111101101111100111110011110000000-----
 -----0-----
 Gyalideopsis_lobulata 00010001000010100001000000110100--10001000-----
 -----01010000000010010100000100-010-100010110-00000-
 000000000010011011111011111001111100000-----
 -----0-----
 Gyalideopsis_megalospora 00100001100010000000000000110100--00001000----
 -----01010000000010000101010000-000----101010010010-000010-
 010110110011110011111000111100000-----
 -----0-----
 Gyalideopsis_mexicana 00100001100010000000100000110100--10001000-----
 -----010100000000111001100010000-000----101000000000-000000-
 01011011001000001100100011100000010000010001000000000000000-----
 -----01000000110001000100-0000-----
 Gyalideopsis_minima 000100100000100100000000000110100--00001000-----
 -----010100000000000010100000000-000----101010010100-000000-0000-
 01100100000110010001100000000-----
 -----0-----
 Gyalideopsis_minutissima 000100100001000000000000001100000--00000-00----
 -----010100000000000110000000000-000----101010000000-001000-
 0000-01100000000100000000100000000-----
 -----0-----
 Gyalideopsis_modesta 010000011010100000000000001100000--00001000-----
 -----01010000000010010100010000-000----010110010100-000010-
 0001001100100000110010001100000000-----
 -----0-----
 Gyalideopsis_monospora 010000011000010000000000000110100--00001000-----
 -----01010000000010000110010000-000----010110010010-000010-
 1101101101111101111100111110000100000100010000000001011100-----
 -----0100000000000000-----0000-----
 Gyalideopsis_montana 000100010001000000000100001100100--10001000-----
 -----01010000000010000110010000-000----010110011000-000000-
 010100110000000011001000110000000100000010000100000000000010-----
 -----?????????????????????????????0-----
 Gyalideopsis_muscicola 001000011010100000000000001100100--00001000-----
 -----01010000000010000101010000-000----101011000000-000011-
 111110110100000011110010011100000100000011000010000100011100-----
 -----00000000000100-----0000-----
 Gyalideopsis_napoensis 010000011000010000000000000110100--00001000-----
 -----010000000000100001000001010000----101000011000-000010-
 010100110011000011001000111000000100000010000010100000011100-----
 -----?????????????????????????????0-----
 Gyalideopsis_nepalensis 010000011010010000000000000110100--00001000-----
 -----010100000100100001010100010000----101010010100-000000-
 000110110010000011001000011000000100000010001000000000001000-----
 -----00000000100010--01000000-----
 Gyalideopsis_ochroleuca 000100100000100000000000001100100--00001000-----
 -----01010000000000010100000000-000----010110000000-000000-
 000100110111110111110011111000000-----
 -----0-----
 Gyalideopsis_pallescens 00010001000010100001000000110100--10001000-----
 -----01000000010010010100000000-000----010110000000-000000-
 01000011011111011111001111100001000000100000000000000000000-----
 -----?????????????????????????????0-----
 Gyalideopsis_pallida 000100100001000000000000001100000--00000-00-----
 -----010100000000000110000000000-000----101010000000-001000-0000-

```

01100000000110010000100000000-----
-----0-----
Gyalideopsis_palmata 00100010000010000000000000110100--00001000-----
-----01000000000000000001010000-000----101010010010-000011-
01111011011111101111100111110000100000011000010001000011100-----
-----00000000100000-----0000-----
Gyalideopsis_parvula 10010111000010-----0-----
-----01010000000000001100001000-000----101010010100-000000-0000-
0100000000000000000000000000-----
-----0-----
Gyalideopsis_perminuta 00010010000010000000000000110100--00001000-----
-----010100000000000010100000010-000----101010010100-000010-0000-
01100000000100000000100000000-----
-----0-----
Gyalideopsis_peruviana 00100001100010000000000000110100--00001000-----
-----01000000010011000100010000-000----101010010100-000011-
0001101100100000111111001110000000-----
-----0-----
Gyalideopsis_philippiae 001000010010100000000000001100100--00001000-----
-----01010000000010001100000010-000----010111010100-000010-
0001001100110000100000000100000000-----
-----0-----
Gyalideopsis_piceicola 00100001011010000000000000110000--00001-00-----
-----01010000010010000101010000-000----010111010010-000011-
000110110011100011001000010000000100000010000010000100000000-----
-----?????????????????????????0-----
Gyalideopsis_puertoricensis 00100010000010001000000000110100--00001000-
-----01010000000010001100010000-000----010110010010-001011-
01011011011111101111100111110000100000010000010000100000000-----
-----0000000010011000001000000-----
Gyalideopsis_robusta 01000010000001000000000000110100--00001000-----
-----011100000000100011000100110000----010110000000-000010-
010110110011100011001000011000000100000000000010000100011100-----
-----00000000000100-----0000-----
Gyalideopsis_rogersii 001000010100100000000000001100100--00001000-----
-----01010000010010000100010000-000----101010000000-000010-
000110110011100011111100111000000100000010000000000000000000-----
-----00001010100000-----0000-----
Gyalideopsis_rostrata 00100010000010001000000000100100--00001000-----
-----01000000000010000110000000-000----010110010010-000011-
010110110011000011111100111000000100000010100011000000011100-----
-----00000000000000-----0000-----
Gyalideopsis_rubescens 000100100001000100000000011001010100001000-----
-----01010000000000001100010000-000----101010010100-001010-
0001001101111110111111001111000000-----
-----0-----
Gyalideopsis_rubra 000100010001000000000000001100100--00001000-----
-----01010000000000001100010000-000----101010000000-001011-
0001101100100000111010000111000000-----
-----0-----
Gyalideopsis_rubrofusca 00100001000100001000000000110100--00001000-----
-----01010000010010001100010000-000----010110000000-000011-
110110110011100011111100111000000100000010000010000100001000-----
-----?????????????????????????0-----
Gyalideopsis_stipitata 00100001100010000000000000110100--00001000-----
-----01110000000010000100010000-000----010110010100-000010-
010110110111111011111100111100000100000100010000000000011000-----
-----01000000000100-----0000-----

```


Gyalideopsis_subantarctica 01000001100001001000000000101000--00001000--
 -----01010000010010000101010000-000----010100011000-000000-
 10011011001110001111100111100000-----
 -----0-----
 Gyalideopsis_triseptata 00010010000100010000000001100100--00001000-----
 -----01010000000000010100010000-000----101010010000-000000-0000-
 01100000000100000000100000001000000100000000000000011100-----
 ?????????????????????????????0-----
 Gyalideopsis_vainioi 00100010000010001001000000110100--10001000-----
 -----010000000101100001100101010000----010100010100-000010-
 0101101101111101111100111110000100000011000010000100011100-----
 -----00000000100000-----0000-----
 Gyalideopsis_verruculosa 00010010000010000000100001010100--10001000-----
 -----01010000000000010100010000-000----101010011000-000000-
 0001001101111101111100111100000100000010000000000000011100-----
 -----00000000100000-----0000-----
 Gyalideopsis_vezdae 001000110000100010000000000110100--00001000-----
 -----01010000000010000100000000-000----010110010100-000010-
 00010011001110001111100111100000100000000000010000100011100-----
 -----00000000000000-----0000-----
 Gyalideopsis_williamsii 001000100000100000000000000110100--00001000-----
 -----01110000000010000101010000-000----010110010010-000011-
 000110110011000011111100111000000100000011000010000100001000-----
 -----000000000000100-----0000-----
 Gyalideopsis_wirthii 001000100000100000000000000110100--00001000-----
 -----01010000000010010100010010-000----010110010100-000000-
 0001001101111101111100111100000100000011000010000100001000-----
 -----00000000110001000100-0000-----
 Hippocrepidea_nigra 0001000100001010000000010010101110010001000-----
 -----01000000000010000011010100-000----101010000000-000010-
 110110110000000010000000011000000101110-----
 00110000000101--00100000100000011000-0000-----
 Jamesiella_perlucida 001000000000100000000000001100100--00001000-----
 -----01010000000000110000000000-000----101010000000-000000-0000-
 011011111011111100111110000100101-----
 00-----10-----
 Jamesiella_scotica 00100001101100000000000000110100--00001000-----
 -----01010000010010001100010000-000----101011010100-000010-
 10011011011111001111100111110000100101-----
 ---11-----10-----
 Linhartia_albomaculans 00010011000001100100000000010100--00000110-----
 -----010100010000100000010100000000----
 10100000011000000110100110001000000000000000000000100000100-----
 -----0-----
 Linhartia_guajalicensis 00010011000001100100000000010100--00000110-----
 -----010100010000100000010100000000----
 111100000110000001101001100010000000000000000000000100000000-----
 -----0-----
 Linhartia_gyalideoides 00010011000001100100000000010100--00000110-----
 -----010100010000000100100010000000----
 101000010000000001101000000010000000000000000000000000000000000000-----
 -----0-----
 Linhartia_philippinensis 00010011000001100100000000010100--00000110-----
 -----010100010000100100110100000000----
 101000010110000001101000000010000000000000000000000000000000000000-----
 -----1010000000-----
 Linhartia_varieseptata 00010011000001100100000000010100--00000110-----
 -----010100010000000100100010000000----

```

10100001011000000110100000001000000011100000011000000-----
-----0-----
Lithogyalideopsis_aterima 010000011010010000000000000110000--00001000--
-----01010000000010001001010010-000---010111010010-000011-
000110100010000010000000110000000100000010000000000000011100-----
-----00001010100000-----0000-----
Lithogyalideopsis_poeltii 010000100000010000000000000110000--00001000--
-----01010000010010000100010000-000---010111010100-000010-
000110110010000010000000010000000100000010000000000000011000-----
-----00001010100000-----0000-----
Lithogyalideopsis_vivantii 010000011010010010000000000110100--10001000--
-----01010000000010001001010000-000---010111010010-000011-
100110110000000000000000010000000100000010000000000000011100-----
-----00001010100000-----0000-----
Lithogyalideopsis_zeylandica 010000011010010000000000000110000--
00001000-----01010000000010000101010000-000----
101010010010-000011-
000110110010000010000000010000000100000010000000000000011100-----
-----00001010100000-----0000-----
Microlychnus_epicorticis 001000000011100000000000000110100--00001000----
-----00-----
-----1000001000010000000000011000-----
-00000000000100-----0000-----
Microspatha_glauca 001000100101100000000000000110100--00001000-----
-----00-----
-----100000000000010100000011100-----
00000000100000-----0000-----
Paratricharia_paradoxa 00010010000100001000000001100100--
000010011100011001000---01000001000000110000001010-00101010000-----
-11100000000-01100000000100000000100000000-----
-----0-----
Phallomyces_palmae 00010010000010010000000001100100--00001000-----
-----00-----
-----100000010000000000000001000-----
00000001100010001000-0000-----
Psathyromyces_rosacearum 00010010000100000000000001100100--
000010010100000001000---00-----
-----100000100000010010000001000---
-----00000000100000-----0000-----
Rubrotricha_helminthospora 00010010000100000000000001100100--
000010010100100001001101001010000000000010100001010-000----
101010000000-000000-0000-
0110010000011100010011100000100000100000010000100010000-----
00000000100000-----0000-----
Sporocybomyces_pulcher 00010010000110000001000001010100--
100010010100000000000---00-----
-----100000010000100000000001000---
-----0000000000000100100100000-----
Tricharia_atrocarpa 00010001000010010000000001100100--
000010011100011000000---01010000000000000001010010-000----
010110010010-001011-0111101100000000100000000100000000-----
-----0-----
Tricharia_aulaxiniformis 00010010000100000000000001100100--
000010011100011000000---01010000010000110000001000-000----
010110010010-001011-0000-
0100000000000000000000000100000010000011000000011100-----
????????????????????????????0-----

```

Tricharia_aulaxinoides 00010001000010000001000001010100--
100010011100011000000----01000000000000000001010010-010-101010111-
10010-
000011001011011001110001111110011110000010000001000000000000011100----
-----0000000110011000001000000-----
Tricharia_bambusae 00100010000100000000000001100100--
100010011100011001000----010100000000100001100100110000----
010110010100-001110-
00011011011100001110001001110000010000001000000000000011100-----
-----?????????????????????????0-----
Tricharia_cuneata 00010000000010010000000001100100--
000010011100011000000----01010000000010000100010010-000----
101010010010-001011-
000110110011100011001000011000000100000010000011000000011100-----
-----00000000100000-----0000-----
Tricharia_demoulinii 00010010000100010000000001100100--
000010011100011000010----0101000000000000001000000010000----
101010010100-000000-
0001001101111101111100111100000100000010000000000010011100-----
-----?????????????????????????0-----
Tricharia_elegans 00010010000100010000000001100100--
000010011100011010010----010100000000000001100010000-000----
101010011000-000000-0001101100111110111111001111000000-----
-----0-----
Tricharia_elegans-hyphophores 00010010000100010000000001100100--
000010011100011010000----010100000000000001100010000-000----
101010011000-000000-
00011011001111101111100111100000100000010000000000010011100-----
-----?????????????????????????0-----
Tricharia_kashiwadani 00010000000100000000000001100100--
100010011100011010000----010000000000100001000100011010-101101010-
00000-0110000100110110111110111111001111100000-----
-----0-----
Tricharia_novoguineense
0001001000010000000100000110010101100010011100011001000----
01010000010000000110000000-000----101010010100-000000-
11010011000000000000000010000000100000010000000000000011100-----
-----00000010100000-----0000-----
Tricharia_pallida 00010010000100000000000001100100--
000010011100011010000----01010000010010110000000010-000----
010110000000-000000-0000-
011001110001111110011100000010000001000000000000011100-----
00000000100000-----0000-----
Tricharia_pseudosantessonii 00010001000010000000100000110100--
100010011100011010000----01010000000010000101010000-000----
101010000000-001010-010110110010000011001000111000000-----
-----0-----
Tricharia_santessoniana 00010010000100010000000001100100--
000010011100011000000----01110000000000110000001010-000----
101010000000-001000-0000-
0110010000010000000010000001000000000000000000011100-----
00000000100000-----0000-----
Tricharia_santessonii 00010010000100010000000001100100--
000010011100011000000----01010000000010000101010010-000----
101010000000-001000-000100110011000011001000011000000-----
-----0-----
Tricharia_sublancicarpa 00010010000010010000000001100100--
000010011100011001000----01000000000010000100010010-010-101101010-

```

00000-
0011110000110110111111011111100111110000100000000000000000000011100----
-----0000000??????????????0??0-----
Tricharia_substipitata 00010010000100000000000001100100--
000010011100011001000----01110000000010010100000010-000----
010110000000-000000-1000-
0110011110011111110011110000100000010000000000010011100-----
?????????????????????????0-----
Tricharia_testacea 00100010000010000000000000110100--
000010010100000001000----010000000000100110000000010000----
101000011000-000000-
000100110000000011001000111000000100000000000010000100001000-----
-----?????????????????????????0-----
Tricharia_triseptata 000100100001000100000000001100100--
000010011100011010000----010100000000000010100010000-000----
101010000000-000000-0000-01100000000100000000100000000-----
-----0-----
Tricharia_umbrosa 001000100000100000000000000110100--
000010011100011010001011001010000000010000101010010-000----
010110010010-001011-0111101101111100111111001111100000-----
-----0-----
Tricharia_variratae 00010010000100000000000001100100--
000010011100011000000----01110000000010010100001000-000----
101010000000-000000-0000-
0110010000011001000110000000100000010000000000010011100-----
?????????????????????????0-----
Tricharia_vezdae 001000000000100010000000000110100--
000010011100010000000----01000000000010000101010000-000----
101000011000-000010-
100110110011100011111100111000000100000000000011000000011100-----
-----00000000100100-----0000-----

```

Capítulo 4

The genus *Gyalideopsis* (lichenized Ascomycota: Gomphillaceae) in Brazil:
updated checklist, key to species, and two novel taxa with unique hyphophores

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): 032–040.

**The genus *Gyalideopsis* (lichenized Ascomycota: Gomphillaceae) in Brazil:
updated checklist, key to species, and two novel taxa with unique
hyphophores**

Amanda Barreto Xavier-Leite^{1,5}, Marcela E. da Silva Cáceres², Bruno Tomio Goto³
and Robert Lücking⁴

¹ *Programa de Pós-Graduação em Sistemática e Evolução, CB, Universidade Federal do Rio Grande do Norte, Campus Universitário, 59072-970, Natal, RN, Brazil;* ² *Departamento de Biociências, Universidade Federal de Sergipe, CEP: 49500-000, Itabaiana, Sergipe, Brazil;* ³ *Departamento de Botânica e Zoologia, CB, Universidade Federal do Rio Grande do Norte, Campus Universitário, 59072-970, Natal, RN, Brazil;* ⁴ *Botanischer Garten und Botanisches Museum, Freie Universität Berlin, Königin-Luise-Strasse 6–8, 14195 Berlin, Germany*

ABSTRACT. We provide a checklist and a key to the 26 species and one infraspecific taxon of the genus *Gyalideopsis* (Gomphillaceae) currently known from Brazil, including two species with unique hyphophores described as new to science herein: *G. aptrootii* Xavier-Leite, M.Cáceres & Lücking sp. nov., characterized by adnate, crescent-shaped hyphophores with moniliform diahyphae and broadly sessile, dark grey-brown apothecia with single, muriform, rather small ascospores; and *G. marcellii* Xavier-Leite, M.Cáceres & Lücking sp. nov., with mussel-shaped hyphophores similar to those of *G. haliotidiformis* but differing in the filiform

⁵ Corresponding author's e-mail: amandabxleite@hotmail.com
DOI: 10.1639/0007-2745-121.1.xxx

diahyphae. The other taxa known from Brazil are: *G. aequatoriana* Kalb & Vězda, *G. altamirensis* Lücking & Umaña, *G. applanata* Herrera-Campos & Lücking, *G. argentea* (Mont.) Kalb & Vězda, *G. brevopilosa* (Kalb & Vězda) Lücking, Sérus. & Vězda, *G. cochlearifera* Lücking & Sérus., *G. confluens* Kalb & Vězda, *G. ellipsoidea* A.A. Menezes, M. Cáceres & Aptroot, *G. epithallina* Lücking, *G. glauca* (P. Karst.) Lücking, Sérus. & Vězda, *G. haliotidiformis* Kalb & Vězda, *G. intermedia* Lücking, *G. kalbii* Vězda, *G. lambinonii* Vězda, *G. lecideina* Kalb & Vězda, *G. palmata* Kalb & Vězda, *G. robusta* Kalb & Vězda, *G. rostrata* Kalb & Vězda, *G. rubescens* Vězda, *G. rubrofusca* Kalb & Vězda, *G. vainioi* Kalb & Vězda, *G. verruculosa* Vězda & Hafellner, *G. vezdae* Kalb, *G. vulgaris* (Müll.Arg.) Lücking f. *vulgaris*, and *G. vulgaris* f. *albopruinosa* Lücking.

KEYWORDS. Corticolous, foliicolous, lichenicolous, muscicolous, saxicolous, terricolous.



1. INTRODUCTION

The genus *Gyalideopsis* was first described by Vězda (1972), originally containing four species. Rapidly growing taxonomic knowledge increased the number to 81 by 2006 (Lücking et al. 2006), including the foliicolous species subsequently described by Lücking (2008), but excluding the segregates *Diploschistella* (4), *Ferraroa* (1), *Jamesiella* (4), and *Lithogyalideopsis* (4; Lücking et al. 2005). The recent classification of lichen fungi gives 95 species for *Gyalideopsis* (Lücking et al. 2017), and the current tally is 99 species plus two infraspecific taxa, adding the following, recently established taxa to the 2006 checklist: *G. americana* Lücking & W.R.Buck, *G. bartramiorum* Lendemer, *G. berenice* (Ellis & Everh.) Lücking & W.R.Buck, *G. chibaensis* H.Harada, *G. chicaque* Moncada & Lücking, *G.*

crenulata Coppins & Aptroot, *G. ellipsoidea* A.A.Menezes, M.Cáceres & Aptroot, *G. frahmii* Aptroot & Schumm, *G. halocarpa* P.M.McCarthy & Elix, *G. heardense* Øvstedal, *G. lunata* H.Harada, *G. ozarkensis* Lücking, W.R.Buck & R.C.Harris, *G. pandani* Vězda, *G. pusilla* Lücking & Tønsberg, *G. sessile* W.B.Sanders & Lücking, *G. stereocaulicola* Etayo, *G. subaequatoriana* Lücking & W.R.Buck, *G. submonospora* Lücking & W.R.Buck, *G. vainioi* var. *semicirculata* Lücking & W.R.Buck, and *G. vulgaris* f. *albopruinosa* Lücking (Coppins & Aptroot 2008; Etayo 2010; Harada 2008; Harada & Kawakami 2011; Lendemmer 2017; Lücking & Tønsberg 2016; Lücking et al. 2007; Lumbsch et al. 2011; McCarthy & Elix 2014; Menezes et al. 2013; Øvstedal & Gremmen 2008; Sanders & Lücking 2015; Schumm & Aptroot 2010; Vězda 2007).

Gyalideopsis includes species with mostly sessile to adnate, biatorine or lecideine apothecia and stipitate to squamiform hyphophores (Lücking et al. 2005, 2006). It is considered a heterogeneous taxon, possibly consisting of several lineages in the family Gomphillaceae, likely distinguished by their different hyphophore types (Lücking 2008; Lücking et al. 2004, 2005). The genus exhibits a broad ecology, being found on rock, soil, bark, mosses and leaf surfaces (Lücking et al. 2005, 2006). Unlike other genera in the family, most species of *Gyalideopsis* are not foliicolous, and the various lineages may be basal or derived within the family (Lücking 2008; Lücking et al. 2005). In material of an unidentified corticolous species from Brazil, the photobiont has been identified as *Heveochlorella* (Sanders et al. 2016).

Gyalideopsis is particularly diverse in Brazil and several novel taxa have been described from the country (Kalb 1983; Kalb & Vězda 1988; Menezes et al. 2013; Vězda 1983). Here, we describe two new species with unique hyphophores discovered in Brazilian material, and we take the opportunity to provide an updated synopsis of the genus in Brazil, with a key and illustrations.

2. MATERIAL AND METHODS

The new material was collected in Brazil in the states of Santa Catarina and São Paulo. Identification and descriptive work was carried out at the Botanischer Garten und Botanisches Museum, Freie Universität Berlin, Germany, using a LEICA Zoom 2000 dissecting microscope and a ZEISS Axioscope compound microscope. Sections were mounted in tap water, in which all measurements were also taken. For initial identification, we used the world key to *Gyalideopsis* (Lücking et al. 2006) and the key in the *Flora Neotropica* monograph on foliicolous lichens (Lücking 2008), as well as the *Color Guide to Gomphillaceae* [http://emuweb.fieldmuseum.org/botany/rlg/search_rlg.php], along with selected literature describing further new species of the genus after 2006 (cited above). The same sources were used to assemble the key to the taxa currently known from Brazil. For distribution in the different Brazilian states, we consulted the cited literature as well as the *Global Biodiversity Information Facility* (GBIF; <https://www.gbif.org>) and the *Herbário Virtual da Flora e dos Fungos* of the Brazilian *Institutos Nacionais de Ciência e Tecnologia da Flora e dos Fungos* (INCT; <http://inct.splink.org.br>).

3. RESULTS AND DISCUSSION

Excluding segregates in *Diploschistella*, *Ferraroa*, *Jamesiella* and *Lithogyalideopsis*, 26 species and one infraspecific taxon of *Gyalideopsis* are known from Brazil, along with a report of an unidentified species (**Table 1**). Of these, more than half (15) have been originally described from the country. The highest number of species is known from São Paulo state (12), followed by Minas Gerais (8), Pernambuco (6), Mato Grosso (5) and Sergipe (4). This appears to reflect to a large degree sampling effort and study depth, rather than ecological preferences of the species; for instance, São Paulo and Minas Gerais are among the best

studied Brazilian states with regard to their lichen biota, whereas Rio de Janeiro, with a comparable climate and diversity of vegetation, has been very little studied (Marcelli 1998).

Of the 15 species of *Gyalideopsis* originally described from Brazil, including those introduced herein (**Table 1**), eight have not yet been reported from outside the country; *G. brevipilosa* has been reported from Malaysia (Paukov et al. 2017), *G. confluens* from Mexico and Costa Rica (Kalb & Vězda 1988; Lücking et al. 2006), *G. kalbii* from Bolivia (Flakus et al. 2013), *G. robusta* from Guyana (Sipman 1992), *G. rostrata* from Taiwan (Aptroot & Sparrius 2003), *G. vainoi* from the United States, Mexico and Costa Rica (Kalb & Vězda 1988; Lücking et al. 2006, 2007), and *G. vulgaris* f. *vulgaris* from throughout the Neotropics (Lücking 2008).

Table 1. List of species of *Gyalideopsis* known from Brazil, with reporting sources indicated in parentheses and distribution in Brazilian states given. AP = Amapá, BA = Bahia, CE = Ceará, DF = Distrito Federal, ES = Espírito Santo, GO = Goiás, MG = Minas Gerais, MS = Mato Grosso do Sul, MT = Mato Grosso, PB = Paraíba, PE = Pernambuco, PR = Paraná, RJ = Rio de Janeiro, RO = Rondônia, RS = Rio Grande do Sul, SC = Santa Catarina, SE = Sergipe, SP = São Paulo. Asterisks indicate species originally described from Brazil, with two asterisks indicating species not yet known from outside the country.

Gyalideopsis aequatoriana Kalb & Vězda (Alves 2014; CE)

Gyalideopsis altamirensis Lücking & Umaña (Menezes 2013; this paper; CE, SC)

Gyalideopsis applanata Herrera-Campos & Lücking (this paper; MG, RJ)

***Gyalideopsis aptrootii* Xavier-Leite, M.Cáceres & Lücking sp. nov. (this paper; SC)

Gyalideopsis argentea (Mont.) Kalb & Vězda (Santesson 1952; Kalb & Vězda 1988; Lücking et al. 1999; MG, PE)

- **Gyalideopsis brevopilosa* (Kalb & Vězda) Lücking, Sérus. & Vězda (Kalb & Vězda 1988; Lücking et al. 2005; MT)
- Gyalideopsis cochlearifera* Lücking & Sérus. (Cáceres 1999; Lücking et al. 1999; Lücking & Kalb 2000; Cáceres et al. 2014; Santos et al. 2017; GBIF; INCT; PE, RO, SE, SP)
- **Gyalideopsis confluens* Kalb & Vězda (Kalb & Vězda 1988; Cáceres et al. 2014; GBIF; INCT; GO, MT, RO, SP)
- ***Gyalideopsis ellipsoidea* A.A.Menezes, M.Cáceres & Aptroot (Menezes et al. 2013; CE)
- Gyalideopsis epithallina* Lücking (this paper; MG, RJ)
- ***Gyalideopsis glauca* (P.Karst.) Lücking, Sérus. & Vězda (Karsten 1889; Lücking et al. 2005; this paper; MG, SP)
- ***Gyalideopsis haliotidiformis* Kalb & Vězda (Kalb & Vězda 1988; GBIF; MT)
- Gyalideopsis intermedia* Lücking (Santos et al. 2017; PE)
- **Gyalideopsis kalbii* Vězda (Vězda 1983; GBIF; INCT; SP)
- Gyalideopsis lambinonii* Vězda (Kalb & Vězda 1988; Cáceres et al. 2014, 2017; Cáceres & Aptroot 2016; GBIF; INCT; AP, BA, GO, MT, SE, SP)
- ***Gyalideopsis lecideina* Kalb & Vězda (Kalb & Vězda 1988; MG)
- *****Gyalideopsis marcellii* Xavier-Leite, M.Cáceres & Lücking sp. nov.** (this paper; SP)
- Gyalideopsis palmata* Kalb & Vězda (Cáceres et al. 2014, 2017; SE)
- **Gyalideopsis robusta* Kalb & Vězda (Kalb & Vězda 1988; SP)
- **Gyalideopsis rostrata* Kalb & Vězda (Kalb & Vězda 1988; Cáceres & Aptroot 2016; AP, MS)
- Gyalideopsis rubescens* Vězda (Kalb & Vězda 1988; Lücking 2008; SP)
- ***Gyalideopsis rubrofusca* Kalb & Vězda (Kalb & Vězda 1988; Aptroot 2002; Cáceres et al. 2014, 2017; MG, SE, SP)

**Gyalideopsis vainioi* Kalb & Vězda (Kalb & Vězda 1988; Santos et al. 2017; this paper; BA, GO, MG, MS, SP)

Gyalideopsis verruculosa Vězda & Hafellner (Cáceres 1999; Lücking 2008; PE)

***Gyalideopsis vezdae* Kalb (Kalb 1983; GBIF; INCT; MT)

Gyalideopsis vulgaris (Müll. Arg.) Lücking f. *vulgaris* (Lombardi et al. 1999; Lücking 2008; Cáceres 1999; Santos et al. 2017; GBIF; INCT; this paper; BA, ES, MG, PB, PE, PR, RJ, RO, RS, SP)

Gyalideopsis vulgaris f. *albopruinosa* Lücking (Lücking 2008; this paper; PE)

Gyalideopsis sp. (Mistry 1998; DF)

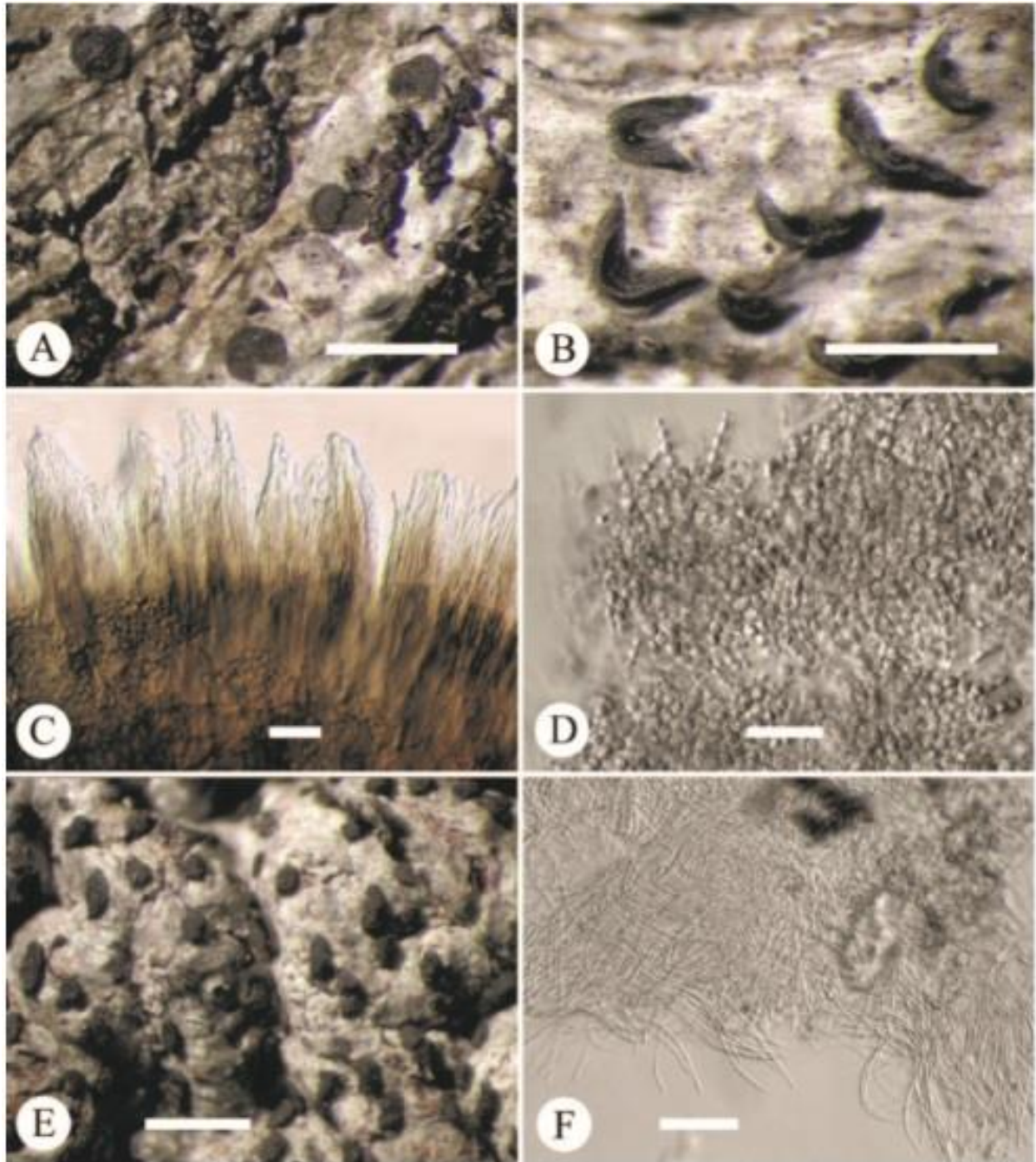


Figure 1. Habit of the new species (holotypes). **A–D.** *Gyalideopsis aptrootii*. **A.** Apothecia. **B.** Hyphophores. **C.** Margin of hyphophore showing partially translucent hyphal scales. **D.** Moniliform diahyphal bunches. **E–F.** *G. marcellii*. **E.** Hyphophores. **F.** Filiform diahyphae. Scale in A, B, E = 1 mm; in C, D, F = 20 μ m.

THE SPECIES

Gyalideopsis aptrootii Xavier-Leite, M.Cáceres & Lücking, *sp. nov.*

Fig. 1A–D

MYCOBANK MB 823947

Differing from other species of Gyalideopsis in the adnate, crescent-shaped hyphophores somewhat resembling those of certain Gyalectidium species and the genus Hippocrepidea.

TYPE: BRAZIL. SANTA CATARINA: São Francisco do Sul, Parque Estadual do Acaraí; 26°19'14.0"S, 48°33'13.0"W, ca. 10 m; Restinga coastal vegetation; 7 October 2015, Cáceres & Aptroot 27836 (ISE, holotype; ABL, B, isotypes).

Description. Thallus corticolous, crustose, continuous, 10–30 mm across and 30–70 µm thick, uneven, with a rather thick, cartilaginous, corticiform layer, lacking clusters of calcium oxalate crystals, white to pale grey, nitidous. Photobiont trebouxoid, cells 5–8 µm diam. Apothecia broadly sessile to almost applanate, biatorine, round, 0.3–0.6 mm diam. and 0.1–0.15 mm high; disc plane, dark brownish grey; proper margin distinct, at the same level of the disc or slightly prominent, of the same color as the disc or somewhat lighter. Excipulum hyphal, 50–100 µm broad, colorless. Hypothecium prosoplectenchymatous, 5–10 µm high, brownish; epithecium indistinct. Hymenium 80–100 µm high, colorless to pale olive-brown in upper parts. Asci broadly clavate, 70–80 × 20–25 µm. Ascospores single, broadly ellipsoid, richly muriform with rather small cells, without constrictions at the septa, 20–35 × 15–20 µm, 1.5–2 times as long as broad, colorless. Hyphophores abundant on thalli without apothecia but also rather frequent on apotheciate specimens, broadly flabellate, crescent-shaped, adnate to the thallus along a broad line on the concave side, 0.1–0.2 mm long in radial direction and 0.5–1 mm broad in tangential direction, blackish grey with a rim of partially translucent, narrow hyphal scales along the convex periphery that attach to the thallus surface. Diahyphae inserted beneath the cavity, forming moniliform clusters attached

through an unbranched, 50–100 μm long and 2.5–3 μm broad, filiform, septate hypha; the terminal, moniliform clusters strongly branched from a single, basal point, segments broadly clavate to drop-shaped or subglobose, 3–5 \times 2.5–3.5 μm , narrower towards the apex, colorless.

Chemistry. No substances detected with TLC.

Etymology. Dedicated to our colleague and friend, André Aptroot, for his numerous contributions to tropical lichenology and his continuous mentorship.

Distribution and ecology. The new species is thus far only known from a well-preserved coastal forest habitat in the extratropical portion of southern Brazil, growing on bark.

Discussion. This new species is characterized by the unique, adnate, crescent-shaped hyphophores with acute edges, together with the single-spored asci with rather small ascospores. The only other species with somewhat similar hyphophores is *Gyalideopsis krogiae* Kalb & Vězda (Kalb & Vězda 1994) from Kenya, in which the hyphophores are flabellate, lacking acute edges, and have a reddish-brown color; *G. krogiae* also agrees in the moniliform diahyphae and the single-spored asci, but its apothecia are white-pruinose with black margins and larger (up to 1 mm diam.), and its ascospores are larger (Lücking et al. 2006). The moniliform diahyphal clusters are reminiscent of those found in the foliicolous genus *Gyalectidium* Müll.Arg. (Ferraro et al. 2001), but lack associated algae; the latter genus also differs strongly in apothecial morphology and anatomy. Somewhat similar hyphophores are also found in the foliicolous, monospecific genus *Hippocrepeida* Sérus. from Papua New Guinea (Aptroot et al. 1997); in that taxon, the hyphophores are narrower and the diahyphae have a different anatomy.

Gyalideopsis marcellii Xavier-Leite, M.Cáceres & Lücking, *sp. nov.*

Fig. 1E–F

MYCOBANK MB 823948

Differing from Gyalideopsis haliotidiformis in the narrower hyphophore scales and the filiform diahyphae.

TYPE: BRAZIL. SÃO PAULO: Pratânia, Fazenda Palmeira da Serra; 22°48'50.0"S, 48°44'35.3"W, 715 m; Cerrado remnant; July 2009, *Lücking 29544* (SP, holotype; B, F, isotypes).

Description. Thallus corticolous, crustose, continuous, 10–30 mm across and 30–60 µm thick, uneven to thinly verrucose, with cartilaginous, corticiform layer and scattered clusters of calcium oxalate crystals, white to pale greenish, slightly nitidous. Photobiont trebouxoid, cells 5–7 µm diam. Apothecia not observed. Hyphophores abundant, broadly flabellate, narrowly ear-shaped to irregular and somewhat resembling insect droppings, broadly attached to the thallus on the basal side, with the peripheral side slightly ascending, 0.1–0.15 mm long in radial direction and 0.3–0.5 mm broad in tangential direction, brownish black. Diahyphae inserted beneath the cavity, filiform, unbranched, emerging from the peripheral side and arranged in a dense, parallel bundle along the roof of the hyphophore scale towards the base, non-septate, 80–100 µm long and 0.7–1 µm broad, colorless.

Chemistry. No substances detected with TLC.

Etymology. We dedicate this new species to our colleague and friend, Marcelo Pinto Marcelli, who has been a modern pioneer of Brazilian lichenology for many decades and has shaped an entire new generation of Brazilian lichenologists.

Discussion. Only few species of *Gyalideopsis* have adnate, broadly flabellate hyphophores, namely *G. haliotidiformis* Kalb & Vězda (Kalb & Vězda 1988), the aforementioned *G. krogiae*, and the newly described *G. aptrootii* above. Most similar in overall aspect is *G. haliotidiformis*, which agrees more or less in hyphophore shape and also lacks apothecia, but its hyphophores are about as long as broad and its diahyphae form

bacilliform segments with slight constrictions, thus appearing sausage-shaped (akin towards moniliform). *Gyalideopsis aptrootii* differs in the moniliform diahyphae (with more or less clavate segments), in addition to its hyphophores being crescent-shaped with acute edges; *G. krogiae* can also be distinguished by its moniliform diahyphae (with more or less globose segments), in addition to its hyphophores being reddish brown.

***Gyalideopsis altamirensis* Lücking & Umaña**

Discussion. This material agrees with *Gyalideopsis altamirensis* in the applanate, dark grey-brown, non-pruinose, rather small (up to 0.6 mm diam.) apothecia and the single-spored asci with muriform ascospores about $50 \times 30 \mu\text{m}$ large. Morphologically and anatomically similar apothecia are known from *G. gigantea* Kalb & Vězda (Kalb & Vězda 1994), which differs, however, in the unusually large hyphophores with pilose stipe.

Specimens seen. BRAZIL. SANTA CATARINA: São Francisco do Sul, Parque Estadual do Acaraí; $26^{\circ}19'14.0''\text{S}$ $48^{\circ}33'13.0''$, ca. 10 m; Restinga coastal vegetation; 7 October 2015, Cáceres & Aptroot 27838 (ISE).

***Gyalideopsis applanata* Herrera-Campos & Lücking**

Specimens seen. BRAZIL. RIO DE JANEIRO/MINAS GERAIS: Parque Nacional do Itatiaia (PNI); $22^{\circ}30'33''\text{S}$, $42^{\circ}15'19''\text{W}$, 600 m; Atlantic forest; May 2015, Xavier-Leite 1321 (ISE).

***Gyalideopsis epithallina* Lücking**

Specimens seen. BRAZIL. RIO DE JANEIRO/MINAS GERAIS: Parque Nacional do Itatiaia (PNI); 22°30'33"S, 42°15'19"W, 600 m; Atlantic forest; May 2015, *Xavier-Leite 1030* (ISE).

***Gyalideopsis glauca* (P.Karst.) Lücking, Sérus. & Vězda**

Discussion. This taxon was originally described from Brazil and is so far only known from its conspicuous hyphophores. The newly collected material is very rich and typical but also lacks apothecia.

Specimens seen. BRAZIL. SÃO PAULO: Pratânia, Fazenda Palmeira da Serra; 22°48'50.0"S, 48°44'35.3"W, 715 m; Cerrado remnant; July 2009, *Lücking 29590* (B, F, SP).

***Gyalideopsis vainioi* Kalb & Vězda**

Specimens seen. BRAZIL. SÃO PAULO: Pratania, Fazenda Palmeira da Serra; 22°48'50.0"S, 48°44'35.3"W, 715 m; Cerrado remnant; July 2009, *Lücking 29598* (B, F, SP).

Gyalideopsis vulgaris* (Müll.Arg.) Lücking f. *vulgaris

Specimens seen. BRAZIL. ESPÍRITO SANTO: Estação Biológica Santa Lúcia; 19°56'10"S, 40°36'06"W, 650 m; Atlantic forest; September 2015, *Xavier-Leite 2229* (ISE). RIO DE JANEIRO/MINAS GERAIS: Parque Nacional do Itatiaia (PNI); 22°30'33"S, 42°15'19"W, 650 m; Atlantic forest; May 2015, *Xavier-Leite 1188, 1198* (ISE). PARAÍBA: Parque Estadual Mata do Pau-Ferro; 06°58'S, 35°42'W, 400 m; Caatinga forest; August 2014, *Xavier-Leite 1476* (ISE).

KEY TO THE SPECIES OF *GYALIDEOPSIS* KNOWN FROM BRAZIL

- 1a Foliicolous or lichenicolous on foliicolous thalli of Gomphillaceae or Pilocarpaceae..... 2
- 1b Not foliicolous.....9
- 2a Lichenicolous on foliicolous thalli of Gomphillaceae; ascospores 1(–3)-septate;
hyphophores when present black, rostrate or spatulate.....3
- 2b Foliicolous with proper thallus; ascospores (3–)7-septate or muriform; hyphophores
when present whitish or pale, rarely black, always setiform4
- 3a Apothecia yellow; hyphophores rostrate..... *Gyalideopsis epithallina*
- 3b Apothecia black; hyphophores spatulate.....*Gyalideopsis cochlearifera*
- 4a Ascospores (3–)7-septate *Gyalideopsis applanata*
- 4b Ascospores muriform5
- 5a Thallus smooth, lacking calcium oxalate crystals, with reddish brown prothallus;
apothecia brownish red; hyphophores unknown..... *Gyalideopsis rubescens*
- 5b Thallus verrucose, with clusters of calcium oxalate crystals; hyphophores frequently
present6
- 6a Apothecia greenish yellow, with epithelial algae; excipulum paraplectenchymatous;
hyphophores encrusted with crystals, diahyphae intermingled with algal cells7
- 6b Apothecia brownish to orange, without epithelial algae; excipulum hyphal;
hyphophores lacking crystals, diahyphae not associated with algal cells.....8

- 7a Apothecial margin of same color as disc *Gyalideopsis vulgaris* f. *vulgaris*
- 7b Apothecial margin white-pruinose *Gyalideopsis vulgaris* f. *albopruinosa*
- 8a Apothecia yellowish grey; hyphophores pale, diahyphal segments fusiform to citriform; verrucae of same color or paler than the thallus *Gyalideopsis intermedia*
- 8b Apothecia yellowish brown to orange; hyphophores black, diahyphal segments ellipsoid to drop-shaped; thallus verrucae white
..... *Gyalideopsis verruculosa*
- 9a Terricolous; apothecia stipitate, reddish brown with white pruina; ascospores 2–4 per ascus, small muriform; hyphophores hand-shaped, black; diahyphae filiform
..... *Gyalideopsis rostrata*
- 9b Saxicolous, corticolous or muscicolous; apothecia sessile to applanate; ascospores, hyphophores and diahyphae variable 10
- 10a Saxicolous; apothecia pure black; hyphophores unknown *Gyalideopsis lecideina*
- 10b Corticolous or muscicolous; apothecia yellow-brown to brown-black but not pure black; hyphophores and diahyphae variable 11
- 11a Ascospores 3-septate, 11–13 × 5.5–6.5 µm; hypothecium blackish; hyphophores unknown
..... *Gyalideopsis ellipsoidea*
- 11b Ascospores (sub-)muriform, larger, or apothecia absent; hypothecium hyaline to at best brownish; hyphophores and diahyphae variable 12

- 12a Identification by means of apothecia; hyphophores present or absent 13
- 12b Identification by means of hyphophores; apothecia present or absent 25
- 13a Ascospores submuriform, 4–8 per ascus, 15–20 × 7–10 μm; hyphophores capitate;
diahypae filiform; muscicolous.....*Gyalideopsis kalbii*
- 13b Ascospores muriform, 1(–4 per ascus), 20–75 × 10–35 μm; hyphophores variable but
not capitate; diahyphae variable; mostly corticolous, rarely (*G. argentea*) muscicolous
..... 14
- 14a Ascospores (1–)2–4 per ascus, up to 20 μm broad 15
- 14b Ascospores single, usually over 20 μm broad (if narrower, then hyphophores crescent-
shaped) 18
- 15a Ascospores 25–50 × 12–15 μm, about 2–3 times as long as broad; apothecia applanate,
yellow-brown; hyphophores very small, narrowly flabellate, black; diahyphae
moniliform*Gyalideopsis confluens*
- 15b Ascospores 20–40 × 10–20 μm, about 1.5–2 times as long as broad; apothecia variable;
hyphophores conspicuous, spatulate to hand-shaped; diahyphae variable 16
- 16a Ascospores 30–40 μm long; apothecia sessile, pale brown with dark margin;
hyphophores brown-black, hand-shaped; diahyphae filiform.....*Gyalideopsis vezdae*
- 16b Ascospores 20–30 μm long; apothecia variable; hyphophores with pale stipe and
darkened apex; diahyphae moniliform or unknown..... 17
- 17a Apothecia applanate, light brown; hyphophores spatulate; diahyphae moniliform.....

-*Gyalideopsis aequatoriana*
- 17b Apothecia sessile, red-brown; hyphophores hand-shaped; diahyphae unknown.....
-*Gyalideopsis rubrofusca*
- 18a Ascospores 20–35 × 15–20 μm; hyphophores crescent-shaped, grey-black; diahyphae moniliform
-*Gyalideopsis aptrootii*
- 18b Ascospores (30–)40–75 × (18–)20–35 μm; hyphophores variable but not crescent-shaped; diahyphae variable
- 19
- 19a Apothecia with black margins; hyphophores rostrate; diahyphae filiform
-*Gyalideopsis rostrata*
- 19b Apothecia with concolorous or pale margins; hyphophores variable but not rostrate; diahyphae moniliform; or hyphophores absent.....
- 20
- 20a Muscicolous; ascospores 30–40 μm long; hyphophores hand-shaped
-*Gyalideopsis argentea*
- 20b Corticolous; ascospores (35–)40–75 μm long; hyphophores variable, if hand-shaped then apothecia white-pruinose.....
- 21
- 21a Apothecia white-pruinose; hyphophores hand-shaped
-*Gyalideopsis vainioi*
- 21b Apothecia non-pruinose; hyphophores variable but not hand-shaped
- 22
- 22a Apothecia purplish brown; ascospores up to 70 μm long; hyphophores unknown
-*Gyalideopsis altamirensis*
- 22b Apothecia brown-black; ascospores up to 60 μm long; hyphophores variable
- 23

- 23a Hyphophores adnate, radiately umbellate *Gyalideopsis lambinonii*
- 23b Hyphophores bristle-shaped to palmate 24
- 24a Hyphophores bristle-shaped, white *Gyalideopsis brevopilosa*
- 24b Hyphophores palmate, red-brown *Gyalideopsis palmata*
- 25a Hyphophores adnate, squamiform or umbellate 26
- 25b Hyphophores bristle-shaped or stipitate and apically widened, sometimes with reduced
stipe 29
- 26a Hyphophores adnate, radiately umbellate *Gyalideopsis lambinonii*
- 26b Hyphophores squamiform, mussel-shaped to crescent-shaped 27
- 27a Hyphophores crescent-shaped; diahyphae moniliform *Gyalideopsis aptrootii*
- 27b Hyphophores mussel-shaped; diahyphae variable 28
- 28a Diahyphae filiform *Gyalideopsis marcellii*
- 28b Diahyphae moniliform *Gyalideopsis haliotidiformis*
- 29a Hyphophores bristle-shaped, white *Gyalideopsis brevopilosa*
- 29b Hyphophores apically widened, mostly at least partially dark 30
- 30a Hyphophores capitate, pinkish; diahyphae filiform; muscicolous *Gyalideopsis kalbii*

- 30b Hyphophores variable but not capitate, instead vertically flattened towards the apex;
diahypae variable; corticolous or rarely muscicolous.....31
- 31a Diahypae filiform; apothecia with darker margin32
- 31b Diahypae moniliform; apothecia with concolorous or paler margin33
- 32a Hyphophores rostrate *Gyalideopsis rostrata*
- 32b Hyphophores hand-shaped *Gyalideopsis vezdae*
- 33a Hyphophores very large, up to over 1 mm high and up to 1 mm broad in the upper,
expanded portion..... *Gyalideopsis glauca*
- 33b Hyphophores small, less than 0.5 mm high and broad34
- 34a Hyphophores with entire or very finely dissected margins.....35
- 34b Hyphophores hand-shaped, with coarsely dissected margins36
- 35a Hyphophores fin-shaped to palmate..... *Gyalideopsis palmata*
- 35b Hyphophores narrowly spathulate *Gyalideopsis aequatoriana*
- 36a Hyphophores with pale stipe, darkened in upper part..... *Gyalideopsis rubrofusca*
- 36b Hyphophores entirely brown-black.....37
- 37a Ascospores 1–4 per ascus, 12–15 μm wide *Gyalideopsis confluens*
- 37b Ascospores single, 18–35 μm wide.....38

38a Ascospores 35–75 μm long; apothecia white-pruinose; corticolous*Gyalideopsis vainioi*

38b Ascospores 30–40 μm long; apothecia non-pruinose; muscicolous ... *Gyalideopsis argentea*

ACKNOWLEDGMENTS

The Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES is thanked for a PhD scholarship to ABXL. The CNPq – Conselho Nacional de Desenvolvimento Científico e Tecnológico (Processo 207282/2015-3) is thanked for supporting the work abroad at the Botanical Garden and Botanical Museum Berlin Berlin, for funding for the collecting trips (459155/2014-8), and for supporting a collaborative project with RL as Special Visiting Professor (314570/2014-4) and for the research grants to MESC (309058/2015-5) and BTG. We also thank Patrícia Jungbluth and Emerson Gumboski and their teams for assistance with the field work in São Paulo and Santa Catarina. Michel Benatti and Emerson Gumboski kindly helped with arrangements for material exchange.

4. LITERATURE CITED

- Alves, M. M. E. 2014. Levantamento das espécies de líquens em áreas de Cerrado na Chapada do Araripe – CE. Universidade Regional do Cariri, Crato, Brazil.
- Aptroot, A. 2002. New and interesting lichens and lichenicolous fungi in Brazil. *Fungal Diversity* 9: 15–45.
- Aptroot, A. & L. B. Sparrius. 2003. New microlichens from Taiwan. *Fungal Diversity* 14: 1–50.
- Aptroot, A., P. Diederich, E. Sérusiaux & H. Sipman. 1997. Lichens and lichenicolous fungi from New Guinea. *Bibliotheca Lichenologica* 64: 1–220.

- Cáceres, M. E. S. 1999. Líquens foliícolas da Mata Atlântica de Pernambuco (Brasil): Diversidade, ecogeografia e conservação. M.Sc. Thesis, Centro de Ciências Biológicas da Universidade Federal de Pernambuco, Recife, Brazil.
- Cáceres, M. E. S. & A. Aptroot 2016. First inventory of lichens from the Brazilian Amazon in Amapá State. *The Bryologist* 119: 250–265.
- Cáceres, M. E. S., E. L. de Lima, Nascimento, A. Aptroot & R. Lücking. 2014, Líquens brasileiros: novas descobertas evidenciam a riqueza no Norte e Nordeste do país. *Boletim do Museu de Biologia Mello Leitão (N. Ser.)* 35: 101–119.
- Cáceres, M. E. S., A. Aptroot & R. Lücking. 2017. Lichen fungi in the Atlantic rain forest of Northeast Brazil: the relationship of species richness with habitat diversity and conservation status. *Brazilian Journal of Botany* 40: 145–156.
- Coppins, B. J. & A. Aptroot. 2008. New species and combinations in The Lichens of the British Isles. *Lichenologist* 40: 363–374.
- Etayo, J. 2010. Hongos liquenícolas de Perú. Homenaje a Rolf Santesson. *Bulletin de la Société Linnéenne de Provence* 61: 83–128.
- Ferraro, L. I., R. Lücking & E. Sérusiaux. 2001. A world monograph of the lichen genus *Gyalectidium* (Gomphillaceae). *Botanical Journal of the Linnean Society* 137: 311–345.
- Flakus, A., H. J. M. Sipman, K. Bach, P. Rodriguez-Flakus, K. Knudsen, T. Ahti, U. Schiefelbein, Z. Palice, A. Jablonska, M. Oset & Q. R. I. Meneses. 2013. Contributions to the knowledge of the lichen biota of Bolivia 5. *Polish Botanical Journal* 58: 697–733.
- Harada, H. 2008. *Gyalideopsis chibaensis* (lichenized Ascomycota, Gomphillaceae), a new gyalectoid lichen from central Japan. *Lichenology* 7: 25–29.

- Harada, H. & S. Kawakami. 2011. *Gyalideopsis lunata* sp. nov. (lichenized Ascomycota, Gomphillaceae) with rudimentary hyphophores, from Gifuken, central Japan. *Lichenology* 10: 23–28.
- Kalb, K. 1983. *Lichenes Neotropici*, Fascicle VI (nos 201–250). Neumarkt.
- Kalb, K. & A. Vězda. 1988. Neue oder bemerkenswerte Arten der Flechtenfamilie Gomphillaceae in der Neotropis. *Bibliotheca Lichenologica*. 29: 1–80.
- Kalb, K. & A. Vězda. 1994. Beiträge zur Kenntnis der foliicolen Flechten australischer Regenwälder IV. *Bulletin de la Société Linnéenne de Normandie*. Prov. 45: 235–246.
- Karsten, P. A. 1889. Fungi aliquot novi in Brasilia a Dre. Edw. Wainia anno 1885 lecti. *Hedwigia* 28: 190–195.
- 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.
- Lombardi, J. A., A. Salino & F. R. Nascimento. 1999. Líquens e outros organismos epifílicos em *Conchocarpus macrophyllus* J. C. Mikan no Parque Estadual do Rio Doce, Minas Gerais, Brasil. *Revista Brasileira de Botânica* 22: 437–441.
- Lücking, R. 1997. Additions and corrections to the knowledge of the foliicolous lichen flora of Costa Rica. The family Gomphillaceae. *Bibliotheca Lichenologica* 65: 1–109.
- Lücking, R. 2008. Foliicolous lichenized fungi. *Flora Neotropica Monograph* 103: 1–866.
- Lücking, R. & K. Kalb. 2000. Foliikole Flechten aus Brasilien (vornehmlich Amazonien), inklusive einer Checkliste und Bemerkungen zu *Coenogonium* und *Dimerella* (Gyalectaceae). *Botanische Jahrbücher für Systematik* 122: 1–61.
- Lücking, R. & T. Tønsberg. 2016. *Gyalideopsis pusilla* (Gomphillaceae, lichenized Ascomycetes), a new species from southeastern North America. **North American Fungi** 11: 1–4.

- Lücking, R., M. E. S. Cáceres & L. C. Maia. 1999. Revisão nomenclatural e taxonômica de líquens foliícolas e respectivos fungos liquenícolas registrados para o estado de Pernambuco, Brasil, por Batista e colaboradores. *Acta Botanica Brasilica* 13: 115–128.
- Lücking, R., B. L. Stuart & H. T. Lumbsch. 2004. Phylogenetic relationships of Gomphillaceae and Asterothyriaceae: evidence from a combined Bayesian analysis of nuclear and mitochondrial sequences. *Mycologia* 96: 283–294.
- Lücking, R., E. Sérusiaux & A. Vězda. 2005. Phylogeny and systematics of the lichen family Gomphillaceae (Ostropales) inferred from cladistic analysis of phenotype data. *Lichenologist* 37: 123–170.
- Lücking, R., A. Aptroot, L. Umaña, J. L. Chaves, H. J. M. Sipman & M. P. Nelsen. 2006. A first assessment of the Ticolichen biodiversity inventory in Costa Rica: the genus *Gyalideopsis* and its segregates (Ostropales: Gomphillaceae), with a world-wide key and name status checklist. *Lichenologist* 38: 131–160.
- Lücking, R., W. R. Buck & E. Rivas Plata. 2007. The lichen family Gomphillaceae (Ostropales) in eastern North America, with notes on hyphophore development in *Gomphillus* and *Gyalideopsis*. *The Bryologist* 110: 622–672.
- Lücking, R., B. P. Hodkinson & S. D. Leavitt. 2017 ('2016'). The 2016 classification of lichenized fungi in the Ascomycota and Basidiomycota – Approaching one thousand genera. *The Bryologist* 119: 361–416.
- Lumbsch, H. T., T. Ahti, S. Altermann, G. Amo De Paz, A. Aptroot, U. Arup, A. Bárcenas Peña, P. A. Bawingan, M. N. Benatti, L. Betancourt, C. R. Björk, K. Boonpragob, M. Brand, F. Bungartz, M. E. S. Cáceres, M. Candan, J. L. Chaves, P. Clerc, R. Common, B. J. Coppins, A. Crespo, M. Dal-Forno, P. K. Divakar, M. V. Duya, J. A. Elix, A. Elvebakk, J. D. Fankhauser, E. Farkas, L. Itatí Ferraro, E. Fischer, D. J. Galloway, E.

Gaya, M. Giralt, T. Goward, M. Grube, J. Hafellner, J. E. Hernández M., M. A. Herrera Campos, K. Kalb, I. Kärnefelt, G. Kantvilas, D. Killmann, P. Kirika, K. Knudsen, H. Komposch, S. Kondratyuk, J. D. Lawrey, A. Mangold, M. P. Marcelli, B. McCune, M. I. Messuti, A. Michlig, R. Miranda González, B. Moncada, A. Naikatini, M. P. Nelsen, D. O. Øvstedal, Z. Palice, K. Papong, S. Parnmen, S. Pérez-Ortega, C. Printzen, V. J. Rico, E. Rivas Plata, J. Robayo, D. Rosabal, U. Ruprecht, N. Salazar Allen, L. Sancho, L. Santos De Jesus, T. Santos Vieira, M. Schultz, M. R. D. Seaward, E. Sérusiaux, I. Schmitt, H. J. M. Sipman, M. Sohrabi, U. Söchting, M. Z. Søgaaard, L. B. Sparrius, A. Spielmann, T. Spribille, J. Sutjaritturakan, A. Thammathaworn, A. Thell, G. Thor, H. Thüs, E. Timdal, C. Truong, R. Türk, L. Umaña Tenorio, D. K. Upreti, P. van den Boom, M. Vivas Rebuelta, M. Wedin, S. Will-Wolf, V. Wirth, N. Wirtz, R. Yahr, K. Yeshitela, F. Ziemmeck, T. Wheeler & R. Lücking. 2011. One hundred new species of lichenized fungi: a signature of undiscovered global diversity. *Phytotaxa* 18: 1–127.

Marcelli, M. P. 1998. History and current knowledge of Brazilian lichenology. Pages 25–45.

In: M. P. Marcelli & M. R. D. Seaward (eds.), *Lichenology in Latin America: History, Current Knowledge and Applications*. CETESB – Companhia de Tecnologia de Saneamento Ambiental, Estado de São Paulo, São Paulo, Brazil.

McCarthy, P. M. & J. A. Elix. 2014. Two new lichens from Mount Canobolas, New South Wales. *Telopea* 16: 119–125.

Menezes, A. A. 2013. Resposta da comunidade de microlíquens corticícolos a fatores ambientais em duas fitofisionomias. M.Sc. Thesis, Universidade Federal de Sergipe, São Cristóvão, Brazil.

- Menezes, A. A., A. B. Xavier-Leite, A. Aptroot & M. E. S. Cáceres. 2013. New lichen species from the Caatinga in Chapada do Araripe, northeastern Brazil. *The Bryologist* 116: 302–305.
- Mistry, J., 1998. Corticolous lichens as potential bioindicators of fire history: a study in the cerrado of the Distrito Federal, central Brazil. *Journal of Biogeography* 25: 409–441.
- Øvstedal, D. O. & N. J. M. Gremmen. 2008. Additions and corrections to the lichens of Heard Island. *Lichenologist* 40: 233–242.
- Paukov, A., H. J. M. Sipman, M. Kukwa, R. Repin & A. Teptina. 2017. New lichen records from the mountains Kinabalu and Tambuyukon (Kinabalu Park, Malaysian Borneo). *Herzogia* 30; 237–252.
- Sanders, W. B. & R. Lücking. 2015. Three new species of foliicolous Gomphillaceae (lichen-forming ascomycetes) from southern Florida. *The Bryologist* 118: 170–177.
- Sanders, W. B., S. Pérez-Ortega, M. P. Nelsen, R. Lücking & A. de los Rios. 2016. *Heveochlorella* (Trebouxiophyceae): a little-known genus of unicellular green algae outside the Trebouxiales emerges unexpectedly as a major clade of lichen photobionts in foliicolous communities. *Journal of Phycology* 52: 840–853.
- Santesson, R. 1952. Foliicolous lichens – A revision of the taxonomy of the obligately foliicolous, lichenized fungi. *Symbolae Botanicae Upsalienses* 12: 1–590.
- Santos, V. M., R. Lücking & M. E. S. Cáceres. 2017. Líquens foliícolas (Ascomycota) em Brejos de Altitude: novos registros para o Nordeste e para o Brasil. *Iheringia Série Botânica* 71: 367–376.
- Schumm, F. & A. Aptroot. 2010. *Seychelles Lichen Guide*. Beck, OHG, Süssen, Germany.
- Sipman, H. J. M. 1992. Results of a lichenological and bryological exploration of Cerro Guaiquinima (Guayana Highland, Venezuela). *Tropical Bryology* 6: 1–31.

- Vězda, A. 1972. Flechtensystematische Studien VII. *Gyalideopsis*, eine neue Flechtengattung. *Folia Geobotanica et Phytotaxonomica* 7: 203–215.
- Vězda, A. 1983. Zwei neue Arten der Flechtengattung *Gyalideopsis*. *Mitteilungen der Botanischen Staatssammlung München* 19: 151–161.
- Vězda, A. 2007. *Gyalideopsis pandani* (lichenisierte Ascomycota, Gomphillaceae), eine neue Art aus Papua New Guinea. *Bibliotheca Lichenologica* 96: 305–309.

manuscript received October 9, 2017; accepted December 23, 2017.