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# Phylogeny and systematics of the lichen family *Gomphillaceae* (*Ostropales*) inferred from cladistic analysis of phenotype data

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**Abstract:** The phylogeny of the lichen family *Gomphillaceae* sensu Vězda & Poelt was reconstructed by parsimony analysis of a phenotype data matrix including ecological, thallus, apothecial, and hyphophore characters. Two hundred and twenty-eight taxa and 209 characters, grouped into ecology (14), thallus (45), apothecia (83), and hyphophores (67), were included in the analysis. *Gyalidea hyalinescens* (*Asterothyriaceae*) was used as outgroup. Because of the high level of homoplasy (consistency index of all-taxa tree without character weighting CI=0·12), and the resulting uncertainty (generally low support) with respect to group topologies, we accepted both monophyletic clades and paraphyletic grades and only rejected previously proposed classifications if the taxon in question appeared polyphyletic, or if segregate taxa were characterized by functionally independent apomorphies and/or by evidence of radiation. Thus, the following 19 genera (synonyms in brackets) are accepted as a result of this study: *Actinoplaca* (segregate of *Echinoplaca*; isidioid hyphophores), *Aderkomyces* (*Psathyromyces*; segregate of *Tricharia*; white setae, hyphal excipulum), *Aplanocalenia* (segregate of *Calenia*; immersed applanate apothecia), *Arthotheliopsis* (*Phallomyces*; segregate of *Echinoplaca*; smooth thallus, differentiated diahyphae), *Aulaxina* (*Lochomyces*; carbonized apothecia, bristle-shaped hyphophores with palmate diahyphae on prothallus), *Calenia* (*Bullatina*; zeorine apothecia, acute to bristle-shaped hyphophores with moniliform diahyphae), *Caleniopsis* (thick white thallus with dark prothallus, zeorine apothecia, bristle-shaped hyphophores with palmate diahyphae on prothallus), *Diploschistella* (segregate of *Gyalideopsis*; immersed apothecia), *Echinoplaca* (*Spinomyces*, *Sporocybomyces*; crystalline thallus, acute to bristle-shaped hyphophores with moniliform or derived diahyphae), *Ferraroa* (segregate of *Gyalideopsis*; campylidioid hyphophores), *Gomphillus* (vertically elongate apothecia, filiform ascospores), *Gyalectidium* (*Tauromyces*; zeorine apothecia, squamiform hyphophores), *Gyalideopsis* (*Epilithia*, *Microlychnus*, *Microspatha*; chiefly biatorine apothecia, setiform or flabellate hyphophores), *Hippocrepidea* (applanate apothecia, squamiform hyphophores with strongly derived diahyphae), *Jamesiella* (segregate of *Gyalideopsis*; isidioid hyphophores), *Lithogyalideopsis* (segregate of *Gyalideopsis*; lecideine apothecia, bristle-shaped hyphophores with palmate diahyphae), *Paratricharia* (black setae, partly carbonized apothecia with columella), *Rubrotricha* (segregate of *Tricharia*; red-brown setae, hyphal excipulum), and *Tricharia* (*Microxyphiomyces*, *Setomyces*; black setae, proso- or paraplectenchymatous excipulum). The following taxa and combinations are introduced: *Actinoplaca gemmifera* comb. nov. [*Echinoplaca gemmifera*], *Aderkomyces albostrigosus* comb. nov. (*Tricharia albostrigosa*), *A. armatus* comb. nov. (*T. armata*), *A. carneoalbus* comb. nov. (*T. carneoalba*), *A. cretaceus* comb. nov. (*T. cretacea*), *A. cubanus* comb. nov. (*T. cubana*), *A. deslooveri* comb. nov. (*T. deslooveri*), *A. dilatatus* comb. nov. (*T. dilatata*), *A. fumosus* comb. nov. (*T. fumosa*), *A. heterellus* comb. nov. (*Arthonia heterella*; *Lopadium membranula*; *Echinoplaca affinis*), *A. guatemalensis* comb. nov. (*T. guatemalensis*), *A. lobulimarginatus* sp. nov., *A. microcarpus* comb. nov. (*T. microcarpa*), *A. microtrichus* comb. nov. (*T. microtricha*), *A. papilliferus* comb. nov. (*T. papillifera*), *A. planicarpus* comb. nov. (*T. planicarpa*), *A. planus* comb. nov. (*T. plana*), *A. purulhensis* comb. nov. (*T. purulhensis*), *A. ramiferus* comb. nov. (*T. ramifera*), *A. subalbostrigosus* comb. nov. (*T. subalbostrigosa*), *A. subplanus* comb. nov. (*T. subplana*), *A. testaceus* comb. nov. (*T. testacea*), *A. verruciferus* comb. nov. (*T. verrucifera*), *A. verrucosus* comb. nov. (*T. verrucosa*), *Aplanocalenia* gen. nov., *A. inconspicua* comb. nov. (*Heterothecium inconspicuum*; *Calenia inconspicua*), *Arthotheliopsis serusiauxii* comb. nov. (*Echinoplaca serusiauxii*), *A. tricharioides* comb. nov. (*E. tricharioides*), *Caleniopsis aggregata* comb. nov. (*Calenia aggregata*), *C. conspersa* comb. nov. (*Thelotrema conspersa*; *Calenia conspersa*), *Diploschistella lithophila* comb. nov. (*Gyalideopsis*

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*lithophila*), *D. solorinellaeformis* comb. nov. (*G. solorinellaeformis*), *D. trapperi* comb. nov. (*G. trapperi*), *Echinoplaca macgregorii* comb. nov. (*Arthonia macgregorii*), *Ferraroa* gen. nov., *Ferraroa hyalina* comb. nov. (*Gyalideopsis hyalina*), *Gyalideopsis brevipilosa* comb. nov. (*Tricharia brevipilosa*), *G. buckei* nom. nov. (*Tricharia vezdae*), *G. cristata* comb. nov. (*Epilithia cristata*), *G. glauca* comb. nov. (*Microspatha glauca*), *G. puertoricensis* sp. nov., *Jamesiella* gen. nov., *J. anastomosans* comb. nov. (*Gyalideopsis anastomosans*), *J. perlucida* comb. nov. (*G. perlucida*), *J. scotica* comb. nov. (*G. scotica*), *Lithogyalideopsis* gen. nov., *L. aterrima* comb. nov. (*Gyalideopsis aterrima*), *L. poeltii* comb. nov. (*G. poeltii*), *L. vivantii* comb. nov. (*G. vivantii*), *L. zeylandica* comb. nov. (*G. zeylandica*), *Rubrotricha* gen. nov., *R. helminthospora* comb. nov. (*Tricharia helminthospora*), *R. subhelminthospora* sp. nov., *Tricharia atrocarpa* sp. nov., and *Tricharia variratae* sp. nov. A key is presented to all genera of *Gomphillaceae*, and a synopsis of the family classification, with all presently known species, is provided.

## Introduction

Many tropical crustose lichen communities are dominated by taxa now accepted as belonging to the *Ostropomycetidae* or *Ostropales* s. lat.: *Porinaceae*, *Coenogoniaceae*, *Graphidaceae*, *Thelotremataceae*, *Asterothyriaceae*, and *Gomphillaceae* (Sipman & Harris 1989; Henssen & Lücking 2002; Kauff & Lutzoni 2002; Lücking *et al.* 2004; Lumbsch *et al.* 2004; Grube *et al.* 2004; Lutzoni *et al.* 2004; Persoh *et al.* 2004). These families have rarely been considered in evolutionary studies of the Ascomycota (e.g. Gargas *et al.* 1995; Lutzoni *et al.* 2001), probably because of the difficult accessibility of their tropical habitats and the largely unresolved taxonomy of these groups. Most of the families above are in need of critical generic treatments to replace the currently existing, largely artificial concepts, with the outstanding revision of *Graphidaceae* by Staiger (2002) having set the standard for further studies in these groups.

Variation due to free or adaptive radiation is one of the most fascinating evolutionary phenomena. In lichenized fungi, such variation seems to be observed best at the taxonomic level that we recognize as family, but it can only be properly addressed if the taxa in question are natural. For example, recurrent evolution of foliose and fruticose from crustose forms in the core *Lecanorales* has been recognized only recently, after Zahlbruckner's artificial system was abandoned in favour of a natural classification based on anatomical and molecular characters (Hafellner 1984; Ekman 2001; LaGreca & Lumbsch 2001; Andersen & Ekman 2004, 2005). On the other hand, the same 'radiative' variation has long been known from widely accepted natural groups, such as the *Physciaceae* and *Teloschistaceae*. From these examples it is obvious that characters used to delimit large groups may in fact vary greatly even within closely related taxa. Indeed, the modern circumscription of *Lecanoromycetidae* and *Ostropomycetidae* demonstrates that virtually no character can be used *a priori* to define a group (Lutzoni *et al.* 2004; Grube *et al.* 2004). Instead, it is essential to understand natural taxa as dynamic entities in which character complexes vary from a basic scheme. Unfortunately, potential homoplasy resulting from this variation makes taxonomy at the generic level difficult and often arbitrary (Lumbsch 2002), as exemplified by the aforementioned *Physciaceae* and *Teloschistaceae* (Kärnefelt 1989; Kasalicky *et al.* 2000; Lohtander *et al.* 2000; Wedin *et al.* 2000, 2002; Grube & Arup 2001; Nordin & Mattsson 2001; Scheidegger *et al.* 2001; Gaya *et al.* 2003; Søchting & Lutzoni 2003).

*Gomphillaceae* are among those lichenized fungi that can be readily recognized at the family level, although only recently have they been delimited in a modern sense (Vězda 1979; Hafellner 1984; Vězda & Poelt 1987; Lücking 1997; Lücking *et al.* 2004). Its members are important components of tropical lichen communities, particularly on living leaves. *Gomphillaceae* was originally monospecific (Watson 1929), but Vězda &

Poelt (1987) later assigned to it 81 species in ten genera, and at present the family includes nearly 300 species with many more awaiting description. A striking example of the diversity reflected by the rapidly increasing taxonomic knowledge is the genus *Gyalideopsis*, properly recognized nearly 30 years ago with four species, and now comprising more than 80!

Apart from *Pilocarpaceae* (now including *Ectolechiaceae* and *Micareaceae*) in the *Lecanorales*, with their peculiar campylidia (Sérusiaux 1986; Vězda 1986; Lücking 1999, 2004; Andersen & Ekman 2004, 2005), the *Gomphillaceae* are the only lichen family with unique, highly derived and complex conidiomata (Vězda 1979; Sérusiaux & De Sloover 1986; Vězda & Poelt 1987; Ferraro 2004). Thus they provide an excellent model for a comparative evolutionary approach to teleomorph-anamorph relationships and 'radiative' variation of apothecia and conidiomata types. Genera in this family were among the first where different ascospore septation was accepted to occur in closely related species (Santesson 1952). Members of the family abound on a wide array of substrata, such as rock and soil, bark and bryophytes, and particularly living leaves. As such, they provide insight into a variety of evolutionary phenomena and may serve as a model of evolution of lichenized fungi, because of the enormous variation of morphological, anatomical, and ecogeographical features.

Before the *Gomphillaceae* can be used as a model group, it is necessary to clarify the systematic relationships of the family. At present, three problems exist. Firstly, the type genus, *Gomphillus*, seems distant from the homogeneous remainder of the family, in having very elongate asci and filiform-acicular ascospores. The ascus type was interpreted as functionally fissitunicate (Hafellner 1984, 1988) but seems to be derived from the annelasceous type characteristic of the *Ostropales* (Lücking 1997). This problem has been clarified in a recent molecular study, where *Gomphillus* was demonstrated to be closely related to the other genera placed in the family (Lücking *et al.* 2004). Secondly, generic delimitation within the family is uncertain regarding the large genera *Gyalideopsis*, *Echinoplaca*, *Tricharia*, and *Calenia*, since apothecial types and sterile setae used to distinguish these genera may have evolved several times independently. Thirdly, there is no consistent pattern as to teleomorph-anamorph relationships. While in some instances (*Aulaxina*, *Gyalectidium*), natural groups are distinguished by both apothecial and hyphophore features, in others these features do not seem to be correlated, making the assessment of systematically important characters difficult.

In the present paper, we address the problem of generic delimitation within the *Gomphillaceae*, using a cladistic approach to assess the value of phenotype characters previously applied to delimit genera in this family. The study has been based on the following working hypotheses (Sérusiaux & De Sloover 1986; Vězda & Poelt 1987; Sérusiaux 1994; Lücking 1997; Dennetière & Péroni 1998; Henssen & Lücking 2002): (1) hyphophores are the evolutionary key feature of the family, obtained via anagenesis from a *Gyalidea*-like ancestor, and leading to anamorph and subsequent teleomorph radiation; (2) *Echinoplaca*-type apothecia evolved from the *Gyalideopsis*-type (by lateral growth of the proper excipulum), and *Calenia*-type apothecia evolved from the *Echinoplaca*-type (by formation of a secondary thalline margin); (3) sterile setae evolved from setiform hyphophores (by losing the ability to produce diahyphae); (4) the same apothecial and hyphophore types may have evolved independently in different groups, with greater variation near the base of the family, and with the possibility of *Echinoplaca*, *Tricharia* and *Calenia* being potentially polyphyletic; (5) evolutionary radiation in the family is connected with substratum preferences and the invention of the foliicolous growth habit.

Considering the limitations of phenotype data for this type of analysis, we applied a rather conservative concept, only proposing changes when our results were in conflict with previous classifications. We see the results of this study as a hypothesis to be tested by molecular data, which unfortunately are not readily available at this stage. Members of this family require freshly collected material to extract usable DNA, and many critical taxa are known only from their type collections. Therefore, it will probably take several years from now to gather a representative array of DNA sequences.

## Materials and Methods

### Selection of taxa

In order to provide a comprehensive survey, and to prevent any potential bias arising from the exclusion of taxa, most currently known genera and almost all species accepted in the family were included in the study (Appendix 1), including a number of previously undescribed taxa which are described herein (Appendix 3) or in other, forthcoming papers. Species published after 2002 (e.g. Herrera-Campos & Lücking 2002, 2003; Vězda 2003; Lücking *et al.* 2003; Ferraro & Lücking 2003; Herrera-Campos *et al.* 2004; Lendemer & Lücking 2004) have been included only if they contributed potentially new information to generic delimitation in *Gomphillaceae*. Two species currently assigned to *Tricharia* were included in the data set based on the assumption that the observed sterile thallus setae in fact represent hyphophores and the species hence may formally belong in *Gyalideopsis*. These are *Tricharia brevipilosa* (as *Gyalideopsis* '*brevipilosa*') and *Tricharia vezdae* (as *Gyalideopsis* '*buckei*'). A total of 228 taxa are included in the various analyses.

### Definition, compilation and handling of characters and character states

*Character and character state definitions*

Preliminary circumscriptions of all taxa were compiled from original literature, and a basic set of characters and character states was extracted from these data. In a second step, world-wide material from the following herbaria and collections was studied: ABLS, B, BM, CR, F, G, GZU, H, INB, KALB, LG, M, S, STU, TUR, UPS, USJ, hb. Lücking, hb. Vězda. Whenever possible, the type and additional specimens from different regions served as a base for establishing the data matrix. All characters were coded in binary [0/1] fashion, to avoid establishment of complex, subjective multistate characters (e.g. stepmatrices) and to facilitate individual character state weighting (Wiley *et al.* 1991; Poe & Wiens 2000; see also Discussion). This resulted in a total of 209 binary characters, divided into four groups (Appendix 2): (1) ecology (14 characters), (2) thallus morphology and anatomy (45), (3) apothecial morphology and anatomy (83), and (4) hyphophore morphology and anatomy (67 characters). Pycnidial characters are known for a few species only and were not included. We also set up biogeographical characters (distribution) but did not include them in the analysis because, by definition, they may not reflect relationships (e.g. vicariant taxa!). On the other hand, we did not *a priori* exclude characters just because they are either quantitative, autapomorphic, homoplastic, or missing in part of the taxa, as is often done in similar studies (Poe & Wiens 2000).

Quantitative characters, such as ascospore length and width, and length/width ratio, were coded using binary transformation series (Wiley *et al.* 1991). The same coding procedure was applied to ordered qualitative characters, such as ascospore number per ascus. This way, the logical relationships between subsequent states of ordered multistate characters can be maintained in binary coding. Regarding gaps, we distinguished between inapplicable and missing data. Inapplicable data refer to characters that depend on the nature of a given character complex. For example, squamiform hyphophores lack a stipe, and hence all characters that apply to stipe morphology are inapplicable. Missing data refer to characters that are found in structures absent from the collections studied but potentially present in the taxon. For example, apothecia, hyphophores, or diahyphae are unknown in a number of species, and it is impossible to decide whether this is a genuine feature of the taxon or simply reflects lack of knowledge. For this reason, inapplicable data gaps were treated as additional characters ('–'), while missing data gaps where treated as unknown ('?') in the nexus file.

In cases when literature data and data from specimens were in conflict or ambiguous, such as the description of the hyphophore type in *Aulaxina dictyospora* by Vězda (1979: 53) *versus* our collections of the species from Costa Rica, data were coded according to our own observations.

*Character weighting*

*A priori* weighting of individual character states was applied to 86 parsimony informative plus 10 autapomorphic characters (Table 1) and resulted in significant improvement of character congruence for the individual analyses, as indicated by CI values (Table 2). Weights were applied at two levels [2/4], based on (1) variation in closely related taxa, such as ascospore septation; (2) systematic importance in related groups of lichenized fungi (*Asterothyriaceae*, *Graphidaceae*, *Thelotremataceae*); and (3) correlation of functionally unrelated characters among taxa (e.g. colour of setae *versus* excipulum structure). *A priori* character correlation was assessed using a Spearman square correlation matrix for all 209 characters established in Statistica 5.0®. Correlations within functional groups of characters, such as ascospore number *versus* ascospore size, were not taken into consideration (see Discussion for further details).

### PAUP analysis

Trees were reconstructed by means of maximum parsimony using PAUP 4.0b10 (Swofford 2003). Because of its size and to allow comparative approaches, the data set was divided into subsets

TABLE 1. *List of characters to which* a priori *weighting was applied according to systematic importance in related groups of lichenized fungi and correlation of functionally unrelated characters among taxa, as assessed by a Spearman square correlation matrix for all 209 characters. See Appendix 2 for details of character definitions*

| Weight=2 | | Weight=4 | |
|---|---|---|---|
| 15 Thallus dispersed | 159 Hyphophores arrow-shaped | 2 Substratum inorganic | 111 Marginal fissure |
| 16 Thallus <1 mm | 160 Hyphophores mussel-shaped | 3 Substratum organic | 120 Asci cylindrical |
| 17 Thallus >3 mm | 161 Hyphophores hand | 4 Substratum foliicolous | 135 Ascospores filiform |
| 20 Thallus verrucose | 164 Hyphophores umbellate | 18 Thallus convex | 147 Hyphophores squamiform |
| 23 Thallus areolate | 165 Pigmentation basal | 24 Thallus papillose | 148 'Thlasidia' |
| 32 Prothallus present | 166 Pigmentation apical | 25 Thick white layer | 162 Hyphophores hooked |
| 34 Prothallus dark | 167 Carbonization | 31 Thallus zoned | 168 Stipe with crystals |
| 41 Setae present | 187 Mass globose | 35 Calcium oxalate crystals | 169 Stipe hairy/tomentose |
| 46 Setae red-brown | 190 Mass divided | 36 '*furcata*' crystals | 170 Scale present |
| 51 Setae longer than 1 mm | 192 Diahyphae hyphal cord | 37 '*atrofusca*' crystals | 186 Mass bell-shaped |
| 52 Setae lateral branches | 197 Branching basal | 38 '*dilatata*' crystals | 188 Mass applanate |
| 53 Setae apical branches | 199 Differentiation apical | 40 Cellular cortex | 191 Gelatinous matrix |
| 54 Secondary setae | 202 Terminally fusiform | 42 Setae always present | 196 Thickened hyphae |
| 56 Secondary black | 205 Terminally multiseptate | 45 Setae on prothallus | 200 Fusiform end segments |
| 61 Apothecia stipitate | 209 Diahyphae algal cells | 47 Setae black | 208 '*lucernifera*' hyphae |
| 92 Proper margin thin | | 48 Setae stiff | |
| 93 Proper margin thick | | 55 Secondary setae red-brown | [autapomorphies] |
| 94 Mature margin thin | | 63 Apothecia adnate | |
| 95 Mature margin thick | | 64 Apothecia elongate | 19 Thallus bullate |
| 107 Excipulum prosoplectenchymatous | | 65 Apothecia levelled | 59 Soralia present |
| 117 Epithecial algae present | | 66 Apothecia erumpent | 105 Columella present |
| 144 Hyphophores marginal | | 86 Thalline rim | 127 Polyspory present |
| 145 Hyphophores on prothallus | | 88 Algiferous margin | 141 Ascospores spiral |
| 146 Hyphophores setiform | | 90 Strongly prominent | 142 Ascospores clavate |
| 153 Hyphophores capitate | | 91 Carbonized margin | 163 Hyphophores coronate |
| 154 Hyphophores acute | | 98 Expanded margin | 201 Terminally branched |
| 155 Hyphophores thickened | | 106 Excipulum well-developed | 206 Terminally constricted |
| 156 Hyphophores widened | | 108 Excipulum paraplectenchymatous | 207 Flagellate appendages |

TABLE 2. *Taxa and character sets, weighting and tree statistics for the phylogenetic analyses displayed in Figures 1–6 and the corresponding analyses with unweighted characters (trees not shown)*

| Taxa | Characters | PI | Weight (2/4)* | Tree length [steps] | MPT | CI |
|---|---|---|---|---|---|---|
| Representative (70) | all (209) | 186 | weighted (43/53) | 1669 | 1 | 0.34 |
| | | | unweighted | 1037 | 1567 | 0.28 |
| Representative (70) | excl. hyph. (142) | 119 | weighted (21/37) | 1094 | 43 | 0.29 |
| | | | unweighted | 719 | 64 | 0.23 |
| Representative (70) | excl. apos. (126) | 113 | weighted (36/35) | 843 | 9300 | 0.48 |
| | | | unweighted | 447 | 8700 | 0.43 |
| *Gyalideopsis-Gomphillus*-grade (71) | all (209) | 137 | weighted (43/53) | 1076 | 724 | 0.30 |
| | | | unweighted | 760 | 200 | 0.23 |
| *Tricharia-Echinoplaca*-grade (93) | all (209) | 140 | weighted (43/53) | 1431 | 400 | 0.24 |
| | | | unweighted | 966 | 300 | 0.19 |
| *Calenia-Aulaxina*-clade (49) | all (209) | 101 | weighted (43/53) | 632 | 16 | 0.47 |
| | | | unweighted | 416 | 18 | 0.37 |

*number in parentheses indicate number of characters with weights 2 and 4, respectively; PI=number of parsimony informative characters; MPT=number of equally most parsimonious trees; CI=consistency index.

regarding taxa and characters. A total of 70 taxa was selected for a representative analysis of all genera and major groups within the family. This dataset included species for which complete information on apothecial and hyphophore characters was available (with a maximum of five species per genus or infrageneric group), as well as selected species with partial information, if they represented type species of generic names or otherwise particular characters. In addition, separate analyses were performed on three taxa sets representing the three major grades and clades evident from the representative taxa set analysis, with reference to current systematic arrangements of the larger genera *Gyalideopsis*, *Tricharia*, *Echinoplaca*, *Calenia*, and *Aulaxina* (Vězda & Poelt 1987; Lücking 1997). An analysis of the genus *Gyalectidium* has already been presented by Ferraro *et al.* (2001) and will not be repeated here.

Based on our working hypotheses as presented in the Introduction, we selected a species of *Gyalidea* (*G. hyalinescens*) in the *Asterothyriaceae* as outgroup. A sister group relationship has been proposed for *Asterothyriaceae* and *Gomphillaceae* (Lücking 1997, 1999; Henssen & Lücking 2002), and this has not been contradicted (but also not confirmed) by our recent molecular analysis, which places both families on a clade sister to *Thelotremataceae* and *Graphidaceae* (Lücking *et al.* 2004). For the partial taxa sets, we selected *Gomphillaceae* outgroups according to their placement in the representative taxa set tree.

Characters were divided into four sets: (1) ecology, (2) thallus morphology and anatomy, (3) apothecial morphology and anatomy, and (4) hyphophore morphology and anatomy. The representative taxa set was subjected to analysis of partial character sets, to test for conflicts between major character complexes such as apothecia (teleomorph) and hyphophores (anamorph).

The shortest trees were searched by means of heuristic search, using random stepwise addition with 100 replicates and tree-branching-regrafting (TBR) as branch swapping algorithm. If searches resulted in multiple parsimonious trees, strict consensus trees were computed to inspect the degree and nature of conflict between individual trees. The consistency index (CI) was used to estimate the level of homoplasy within resulting trees [the homoplasy index (HI) is the complement of the consistency index]. Bootstrap and Jackknife analyses were performed for all analyses, using 1000 replicates and 75% resampling in case of Jackknife analysis.

## Generic delimitation

We attempted to restrict the number of taxonomic and nomenclatural changes as much as possible, without neglecting the results of our phylogenetic analysis. For the definition of natural entities, we accepted both monophyletic clades and paraphyletic grades. The validity of paraphyletic grades is controversial in many theoretical approaches to cladistics, but in practice paraphyletic entities are often retained to avoid major conflicts with the Linnean rank based taxonomic system. This discussion notwithstanding, rigorous application of the monophyly criterion in phenotype data analyses is in our opinion futile, because of the large amount of potential homoplasy in phenotypic data and the resulting weak statistical support.

We accepted taxa as distinct at the generic level if the following applied: (1) the taxon forms either a monophyletic clade or a paraphyletic grade (except for cases where missing data might explain other results); (2) the taxon exhibits at least two functionally independent synapomorphies compared to its closest relative; (3) the number of species is large enough to demonstrate a significant amount of radiation; and (4) the taxon exhibits characters or character states which are unique in the family.

## Results

### Representative taxa set (70 taxa)

*All characters*

The parsimony analysis of 70 representative taxa across all groups with the complete character set (186 parsimony informative characters) resulted in a single most parsimonious tree with a length of 1669 steps (CI=0·34; Table 2). The backbone and intermediate clades receive little or no bootstrap or jackknife support, while most of the terminal clades receive intermediate to strong support (Fig. 1).

Four major entities can be distinguished: (1) the *Gyalideopsis-Gomphillus* grade (basal, paraphyletic), including *Gomphillus* and most species currently assigned to *Gyalideopsis* (except the *Diploschistella urceolata* and *Gyalideopsis anastomosans* groups, and *G. hyalina*, all in the *Gyalectidium-Actinoplaca* clade); (2) the *Tricharia-Echinoplaca* grade (intermediate, paraphyletic), including all species currently assigned to *Tricharia* and *Echinoplaca* (except the *Actinoplaca strigulacea* group in the *Gyalectidium-Actinoplaca* clade); (3) the *Calenia-Aulaxina* clade (derived, monophyletic), including the bulk of foliicolous taxa with zeorine apothecia (except *Gyalectidium* in the *Gyalectidium-Actinoplaca* clade); and (4) the *Gyalectidium-Actinoplaca* clade (derived, monophyletic), including the *Diploschistella urceolata* group and all taxa with strongly derived hyphophores (*Gyalectidium*, *Hippocrepidea*, the *Gyalideopsis anastomosans* group, *G. hyalina*, and the *Actinoplaca strigulacea* group).

The monophyletic *Gyalideopsis aterrima* group (black apothecia with transversely septate ascospores and bristle-like hyphophores with palmate, moniliform diahyphae; inorganic substrata) takes a basal position in the *Gyalideopsis-Gomphillus* grade. Although it receives no support, its separation from the remainder of the tree (and from *Gyalideopsis* s. str.) is well-supported. Between the *G. aterrima* group and *Gyalideopsis* s. str., *Gomphillus* (vertically elongate apothecia and umbellate hyphophores with filiform diahyphae; muscicolous) is strongly supported as a monophyletic clade. *Gyalideopsis* s. str. forms a paraphyletic grade with three large subgroups (not supported): the monophyletic *G. palmata* group (widened and flattened hyphophores; chiefly corticolous), the paraphyletic *Gyalideopsis africana* group (setiform, capitate hyphophores; chiefly muscicolous; includes the generic type *G. peruviana*), and the paraphyletic *G. verruculosa* group (often crystalline thallus and bristle-shaped hyphophores; chiefly foliicolous). The latter takes an intermediate position between the chiefly non-foliicolous *Gyalideopsis-Gomphillus* grade and the bulk of foliicolous taxa in the family.

The chiefly foliicolous *Tricharia-Echinoplaca* grade contains several, variously supported entities: the *Tricharia urceolata* and *T. vainioi* subgroups (the former strongly supported as monophyletic clade), together forming a paraphyletic *Tricharia* s. str. (black thallus setae, proso- to paraplectenchymatous excipulum, bristle-shaped, black hyphophores), the strongly supported, monophyletic *T. helminthospora* group (red-brown thallus setae, hyphal excipulum, setiform or widened and flattened hyphophores), the paraphyletic *Aderkomyces couepiae* group (white thallus setae, mostly hyphal excipulum, setiform or widened and flattened hyphophores), the monophyletic *Arthotheliopsis hymenocarpoides* group (adnate apothecia, setiform or widened and flattened hyphophores), and the paraphyletic *Echinoplaca epiphylla* group, or *Echinoplaca* s. str. (crystalline thallus, adnate apothecia, setiform or bristle-shaped hyphophores).

In the *Calenia-Aulaxina* clade, the *Bullatina aspidota* group and *Calenia* s. str. form a weakly supported, monophyletic clade sister to a clade containing *Paratricharia paradoxa*, *Calenia inconspicua*, *Calenia conspersa*, *Caleniopsis laevigata*, and *Aulaxina*. The *Caleniopsis laevigata* group and *Aulaxina* are both well-supported as monophyletic clades, and also their sister relationship receives rather strong support.

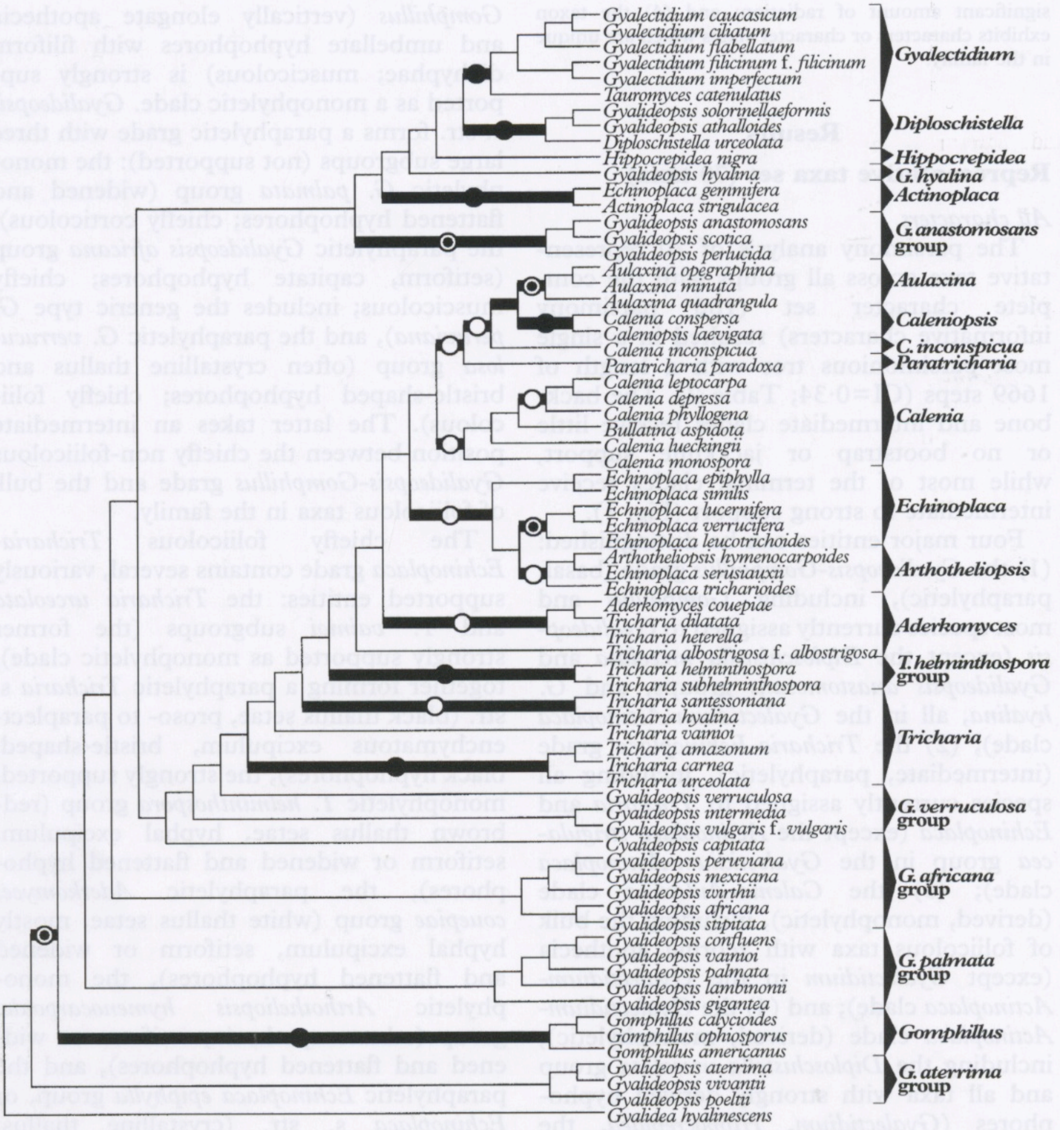



FIG. 1. Single most parsimonious tree (1669 steps) including 70 representative taxa with complete character set (186 parsimony informative characters; CI=0·34). Black/ringed/white dots indicate high (>90%), medium (70–90%), and low (50–70%) average Bootstrap/Jackknife support respectively.

The *Gyalectidium-Actinoplaca* clade has no support *per se* but includes a heterogeneous assemblage of strongly supported, monophyletic groups that mostly have strongly derived hyphophores of different kinds: the *Gyalideopsis anastomosans* group (sessile apothecia, isidioid hyphophores or 'thlasidia'; organic substrata), the *Actinoplaca strigulacea* group (adnate apothecia, isidioid hyphophores; foliicolous), *Gyalideopsis hyalina* (sessile apothecia, campylidioid hyphophores; foliicolous), the monospecific *Hippocrepidea* (applanate apothecia, squamiform hyphophores; foliicolous), and the genus *Gyalectidium* (immersed, zeorine apothecia, hyphophores squamiform; chiefly foliicolous). This clade also includes the *Diploschistella urceolata* group (immersed apothecia; inorganic substrata), although hyphophores are unknown in the selected taxa and not known with certainty from this group. The branch leading to the *Gyalectidium-Actinoplaca* clade is the longest of all basal and intermediate branches (phylogram not shown), which indicates long branch attraction as a possible explanation for the heterogeneous assemblage.

*Excluding hyphophore characters*

When excluding the 67 characters pertaining to hyphophore morphology and anatomy (retaining ecological, thallus and apothecial characters), the parsimony analysis of a subset of 69 taxa (*Echinoplaca gemmifera* removed due to lack of apothecia) yielded 43 most parsimonious trees with a length of 1094 steps each (CI=0·29).

The strict consensus tree (Fig. 2) shows some resemblance with the tree based on all characters, except that the *Gyalectidium* clade is now dissolved and its members distributed among the other grades and clades. The basal, paraphyletic *Gyalideopsis-Gomphillus* grade now includes the strongly supported *Diploschistella urceolata* group and the members of the *G. anastomosans* group (dissolved). The separation between the basal *G. aterrima* and *Diploschistella urceolata* groups and the remainder of the tree (and the bulk of *Gyalideopsis* s. str.) receives intermediate support.

The monophyletic and rather well-supported *Tricharia-Echinoplaca* clade shows roughly the same structure as in the previous tree, although the *Arthotheliopsis hymenocarpoides* group is now paraphyletic and could be included both in a monophyletic *Echinoplaca* s. lat. and in a paraphyletic *Aderkomyces couepiae* group. *Echinoplaca* s. str. is monophyletic, although not supported. The strongly supported, monophyletic *Tricharia helminthospora* group remains in its intermediate position between *Tricharia* s. str. and the *Aderkomyces-Arthotheliopsis-Echinoplaca* clade.

The monophyletic, though weakly supported *Calenia-Aulaxina* clade now includes the monophyletic *Gyalectidium* and thus all chiefly foliicolous taxa with calenioid and aulaxinoid, i.e. immersed and zeorine containing or carbonized apothecia. *Calenia* s. str. and *Aulaxina* remain monophyletic with intermediate to strong support, while the *Caleniopsis laevigata* group is now paraphyletic. *Paratricharia paradoxa* is sister to *Calenia* s. str., while *Calenia inconspicua* takes a basal position as sister to the remainder of this clade. *Hippocrepidea nigra*, *Actinoplaca strigulacea*, and *Gyalideopsis hyalina*, take a position basal to the *Calenia-Aulaxina* clade.

*Excluding apothecial characters*

When excluding the 83 characters pertaining to apothecial morphology and anatomy, the parsimony analysis of a subset of 65 representative taxa (two species of *Gomphillus* and the three species of the *Diploschistella urceolata* group were excluded due to lack of hyphophores and thallus characters) resulted in 9300 equally parsimonious trees with a length of 843 steps each (CI=0·48).

Several differences from the two previous trees can be observed in the strict consensus tree (Fig. 3). The *Gyalideopsis-Gomphillus* grade retains its basal position but is now unresolved, except for the strongly supported separation of the paraphyletic *Gyalideopsis aterrima* group from the remainder of the tree.

The *Tricharia-Echinoplaca* and *Calenia-Aulaxina* clades largely merge to form a monophyletic clade, but now exclude *Aulaxina* and the *Caleniopsis laevigata* group, which in turn form strongly supported, monophyletic clades with an unresolved position. Within the merged *Tricharia-Echinoplaca-Calenia-Aulaxina* clade, several terminal clades receive support: the *Tricharia urceolata* group, the *Tricharia helminthospora* group, a clade including species of *Bullatina*, *Calenia* and *Echinoplaca* with acute hyphophores, and a clade including species of *Echinoplaca* with strongly derived diahyphae. In addition, the *Aderkomyces couepiae* and *Arthotheliopsis hymenocarpoides* groups form a paraphyletic grade, as

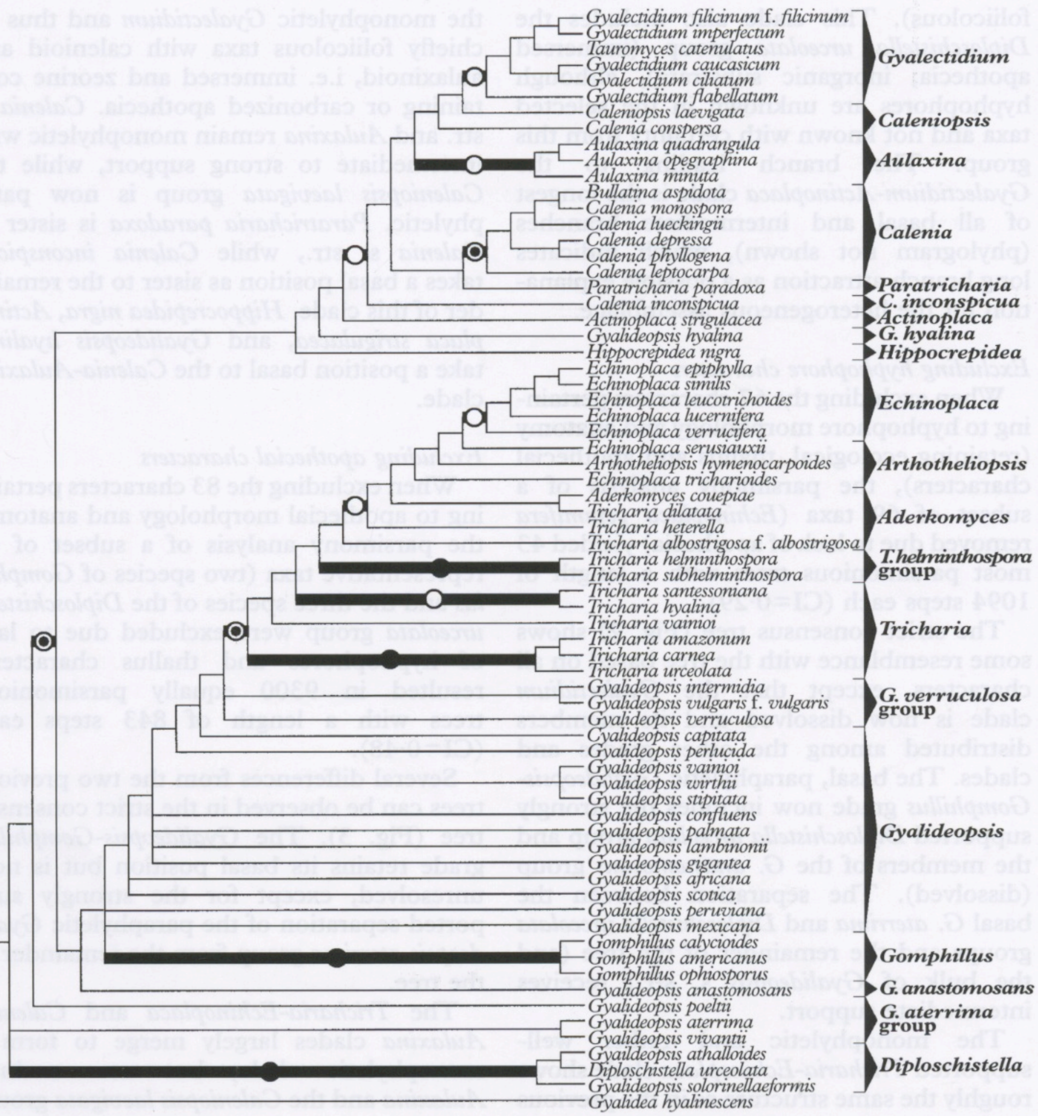



FIG. 2. Strict consensus of 43 equally parsimonious trees (1094 steps) including 69 representative taxa with partial character set exluding hyphophores (142 parsimony informative characters; CI=0·29). Black/ringed/white dots indicate high (>90%), medium (70–90%), and low (50–70%) average Bootstrap/Jackknife support respectively.

do *Tricharia* s. str. (unresolved) and *Calenia* s. str.

The *Gyalectidium-Actinoplaca* clade from the first tree (Fig. 1) is now resolved into three, well-supported clades: a *Gyalectidium* clade also containing *Gyalideopsis hyalina* and *Hippocrepidea nigra*, and two clades containing the *Actinoplaca strigulacea* and *Gyalideopsis anastomosans* groups.

*Congruence and conflict between character sets*

Most of the groups identified in the analysis of all characters are also recovered in the trees after deletion of either hyphophore or

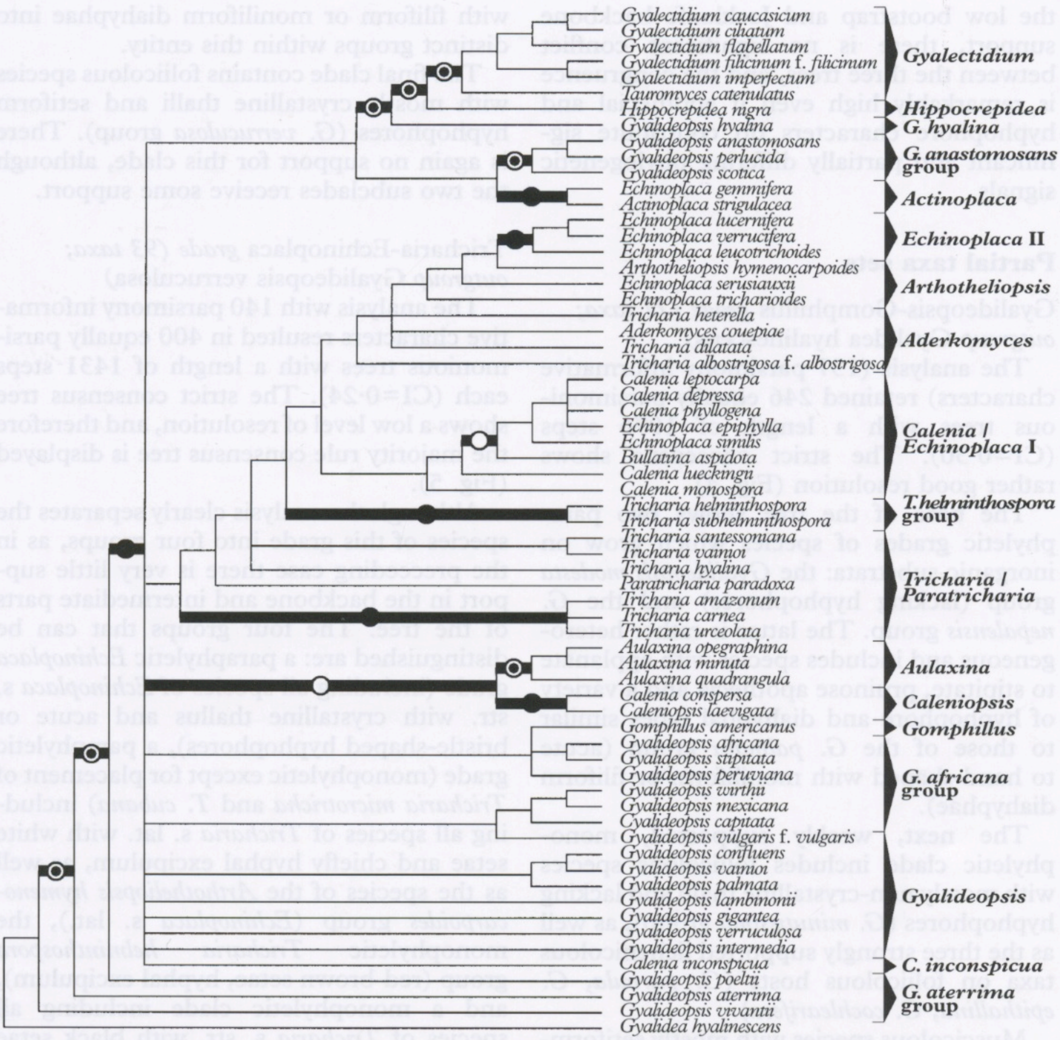



FIG. 3. Strict consensus of 9300 equally parsimonious trees (843 steps) including 65 representative taxa with partial character set exluding apothecia (126 parsimony informative characters; CI=0·48). Black/ringed/white dots indicate high (>90%), medium (70–90%), and low (50–70%) average Bootstrap/Jackknife support respectively.

apothecial characters. The exceptions are: the *Gyalideopsis anastomosans* group (dissolved without hyphophore characters), the *G. palmata* group (unresolved without either hyphophore or apothecial characters), the *G. africana* group (unresolved without hyphophore characters), *Calenia* s. str. (polyphyletic without apothecial characters), and *Echinoplaca* s. str. (polyphyletic without apothecial characters). In addition, the position of several groups changes according to the character set used: thus, the hyphophore-based *Gyalectidium-Actinoplaca* clade dissolves in the analysis lacking hyphophore characters, while the *Tricharia-Echinoplaca* and *Calenia-Aulaxina* grades partly mix in the analysis lacking apothecial characters. On the other hand, considering the low bootstrap and Jackknife backbone support, there is no significant conflict between the three trees, and the congruence is remarkably high even if apothecial and hyphophore characters do contribute significant and partially differing phylogenetic signals.

## Partial taxa sets

Gyalideopsis-Gomphillus *grade (71 taxa; outgroup* Gyalidea hyalinescens*)*

The analysis (137 parsimony informative characters) retained 246 equally parsimonious trees with a length of 1076 steps (CI=0·30). The strict consensus shows rather good resolution (Fig. 4).

The base of the tree shows two paraphyletic grades of species which grow on inorganic substrata: the *Gyalideopsis modesta* group (lacking hyphophores) and the *G. nepalensis* group. The latter is rather heterogeneous and includes species with applanate to stipitate, pruinose apothecia and a variety of hyphophore and diahyphal types similar to those of the *G. palmata* group (acute to hand-shaped with moniliform or filiform diahyphae).

The next, weakly supported, monophyletic clade includes foliicolous species with mostly non-crystalline thalli and lacking hyphophores (*G. minutissima* group), as well as the three strongly supported lichenicolous taxa on foliicolous hosts (*G. parvula*, *G. epithallina*, *G. cochlearifera*).

Muscicolous species with mostly setiform-capitate hyphophores form a paraphyletic grade at the next level of the tree (*Gyalideopsis africana* group). This group includes the type species of the genus, *G. peruviana* (hyphophores unknown), as well as the monospecific *Microlychnus epicorticis*, a hyphophore-based anamorph.

As in the first tree (Fig. 1), *Gomphillus* is strongly supported as a monophyletic clade related to both the *G. africana* and *G. palmata* groups. The latter is here paraphyletic and includes mostly corticolous species with flabellate hyphophores and either filiform or moniliform diahyphae. There is no evidence to support the separation of species with filiform or moniliform diahyphae into distinct groups within this entity.

The final clade contains foliicolous species with mostly crystalline thalli and setiform hyphophores (*G. verruculosa* group). There is again no support for this clade, although the two subclades receive some support.

Tricharia-Echinoplaca *grade (93 taxa; outgroup* Gyalideopsis verruculosa*)*

The analysis with 140 parsimony informative characters resulted in 400 equally parsimonious trees with a length of 1431 steps each (CI=0·24). The strict consensus tree shows a low level of resolution, and therefore the majority rule consensus tree is displayed (Fig. 5).

Although the analysis clearly separates the species of this grade into four groups, as in the preceeding case there is very little support in the backbone and intermediate parts of the tree. The four groups that can be distinguished are: a paraphyletic *Echinoplaca* grade (including all species of *Echinoplaca* s. str. with crystalline thallus and acute or bristle-shaped hyphophores), a paraphyletic grade (monophyletic except for placement of *Tricharia microtricha* and *T. cubana*) including all species of *Tricharia* s. lat. with white setae and chiefly hyphal excipulum, as well as the species of the *Arthotheliopsis hymenocarpoides* group (*Echinoplaca* s. lat.), the monophyletic *Tricharia helminthospora* group (red-brown setae, hyphal excipulum), and a monophyletic clade including all species of *Tricharia* s. str. with black setae and proso- or paraplectenchymatous excipulum.

Within the *Echinoplaca* grade, several more or less well-supported, monophyletic groups can be distinguished: the *E. diffluens* group (coarsely verrucose thallus, large apothecia), the *E. atrofusca* group (dispersed, pruinose thallus, blackish apothecia, hyphophores on prothallus), the *E. leucotrichoides* group (multiseptate terminal diahyphal segments), the *E. furcata* group (coarsely verrucose thallus with branched setae on prothallus, orange apothecia with pruina of needle-shaped crystals, derived diahyphae), and the *E. lucernifera* group

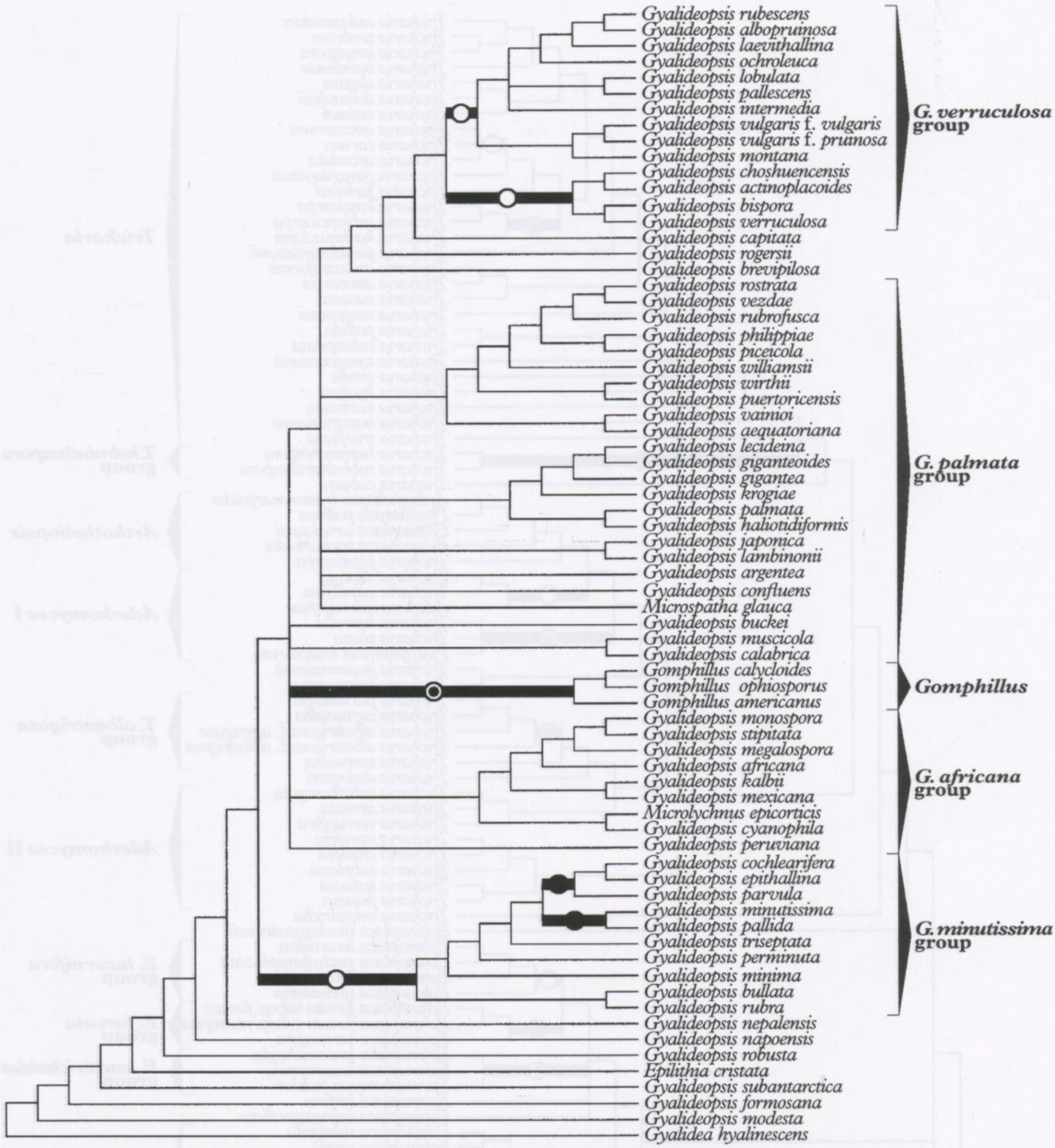
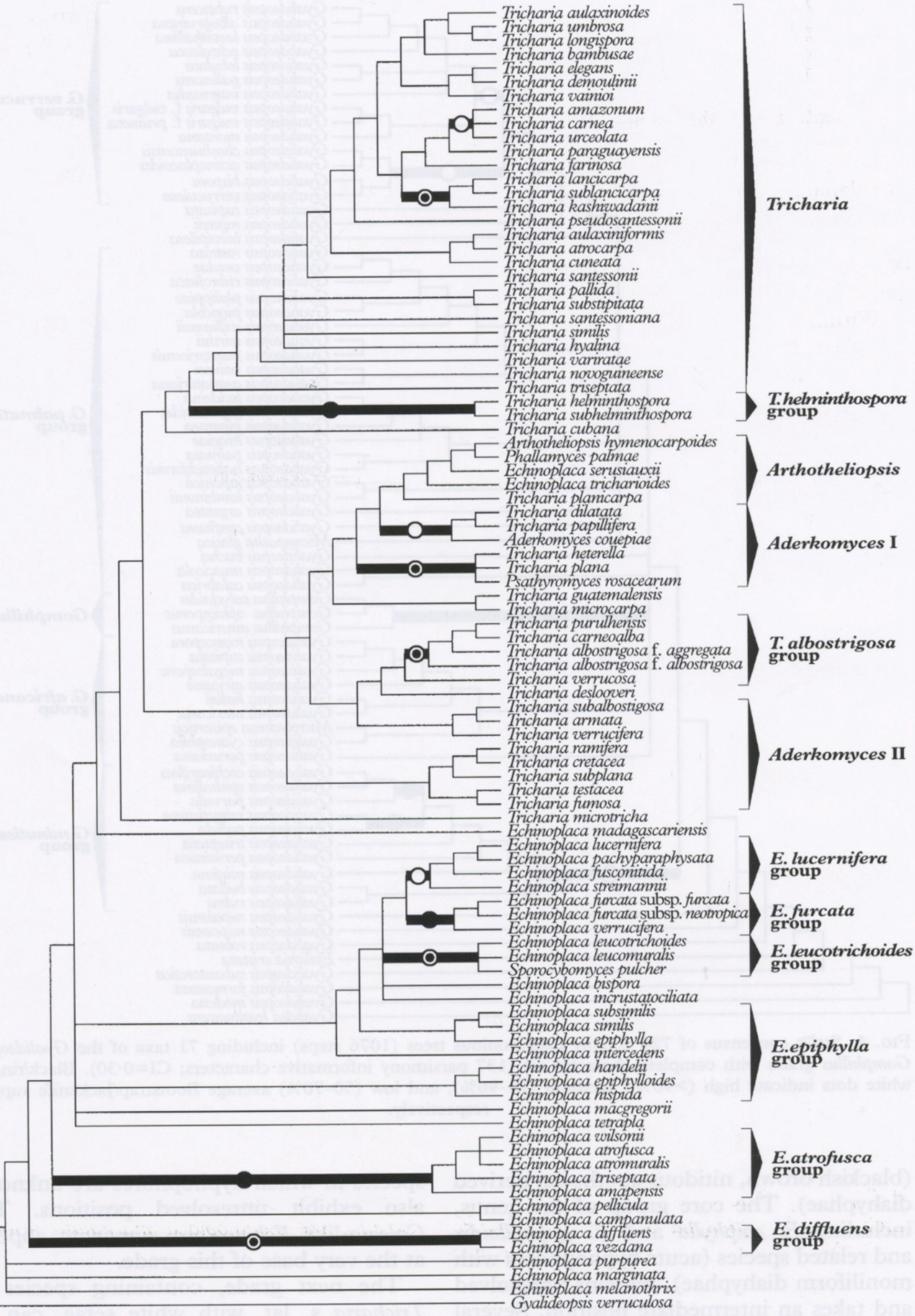



FIG. 4. Strict consensus of 724 equally parsimonious trees (1076 steps) including 71 taxa of the *Gyalideopsis*-*Gomphillus* grade with complete character set (137 parsimony informative characters; CI=0·30). Black/ringed/white dots indicate high (>90%), medium (70–90%), and low (50–70%) average Bootstrap/Jackknife support respectively.

(blackish brown, nitidous apothecia, derived diahyphae). The core group of the genus, including *E. epiphylla* and *E. epiphylloides* and related species (acute hyphophores with moniliform diahyphae), remains unresolved and takes an intermediate position. Several species in which hyphophores are unknown also exhibit unresolved positions. The *Calenia*-like *Echinoplaca marginata* appears at the very base of this grade.

The next grade, containing species of *Tricharia* s. lat. with white setae, can be


Tricharia aulaxinoides
Tricharia umbrosa
Tricharia longispora
Tricharia bambusae
Tricharia elegans
Tricharia demoulinii
Tricharia vainioi
Tricharia amazonum
Tricharia carnea
Tricharia urceolata
Tricharia paraguayensis
Tricharia farinosa
Tricharia lancicarpa
Tricharia sublancicarpa
Tricharia kashiwadanii
Tricharia pseudosantessonii
Tricharia aulaxiniformis
Tricharia atrocarpa
Tricharia cuneata
Tricharia santessonii
Tricharia pallida
Tricharia substipitata
Tricharia santessoniana
Tricharia similis
Tricharia hyalina
Tricharia variratae
Tricharia novoguineense
Tricharia triseptata
Tricharia helminthospora
Tricharia subhelminthospora
Tricharia cubana
Arthotheliopsis hymenocarpoides
Phallamyces palmae
Echinoplaca serusiauxii
Echinoplaca tricharioides
Tricharia planicarpa
Tricharia dilatata
Tricharia papillifera
Aderkomyces couepiae
Tricharia heterella
Tricharia plana
Psathyromyces rosacearum
Tricharia guatemalensis
Tricharia microcarpa
Tricharia purulhensis
Tricharia carneoalba
Tricharia albostrigosa f. aggregata
Tricharia albostrigosa f. albostrigosa
Tricharia verrucosa
Tricharia deslooveri
Tricharia subalbostigosa
Tricharia armata
Tricharia verrucifera
Tricharia ramifera
Tricharia cretacea
Tricharia subplana
Tricharia testacea
Tricharia fumosa
Tricharia microtricha
Echinoplaca madagascariensis
Echinoplaca lucernifera
Echinoplaca pachyparaphysata
Echinoplaca fusconitida
Echinoplaca streimannii
Echinoplaca furcata subsp. furcata
Echinoplaca furcata subsp. neotropica
Echinoplaca verrucifera
Echinoplaca leucotrichoides
Echinoplaca leucomuralis
Sporocybomyces pulcher
Echinoplaca bispora
Echinoplaca incrustatociliata
Echinoplaca subsimilis
Echinoplaca similis
Echinoplaca epiphylla
Echinoplaca intercedens
Echinoplaca handelii
Echinoplaca epiphylloides
Echinoplaca hispida
Echinoplaca macgregorii
Echinoplaca tetrapla
Echinoplaca wilsonii
Echinoplaca atrofusca
Echinoplaca atromuralis
Echinoplaca triseptata
Echinoplaca amapensis
Echinoplaca pellicula
Echinoplaca campanulata
Echinoplaca diffluens
Echinoplaca vezdana
Echinoplaca purpurea
Echinoplaca marginata
Echinoplaca melanothrix
Gyalideopsis verruculosa
Tricharia
T. helminthospora group
Arthotheliopsis
Aderkomyces I
T. albostrigosa group
Aderkomyces II
E. lucernifera group
E. furcata group
E. leucotrichoides group
E. epiphylla group
E. atrofusca group
E. diffluens group

largely divided into four groups: the monophyletic *Arthotheliopsis hymenocarpoides* group (adnate apothecia, differentiated diahyphae), the monophyletic *Tricharia albostrigosa* group (sessile apothecia, moniliform diahyphae), the paraphyletic *Aderkomyces couepiae* group or *Aderkomyces* I (applanate apothecia, moniliform diahyphae), and a paraphyletic group centred around *Tricharia cretacea* and here called *Aderkomyces* II (same features as *Aderkomyces* I but often with a crystalline thallus).

Within the *Tricharia* s. str. clade, there is no clear separation into groups. The *T. urceolata* group (long setae, paraplectenchymatous excipulum; including *T. amazonum*, *T. carnea*, and *T. paraguayensis*) appears monophyletic but excludes the related *T. longispora*. Species with lobulate apothecial margins (*T. lancicarpa*, *T. kashiwadanii*, *T. sublancicarpa*) form a monophyletic clade, while taxa with hooked hyphophores or setae do not group together (e.g. *T. variratae*, *T. elegans*).

Calenia-Aulaxina *clade (49 taxa; outgroup* Echinoplaca epiphylloides*)*

The analysis with 101 parsimony informative characters resulted in 16 equally parsimonious trees with a length of 632 steps each (CI=0·47). The strict consensus tree shows a low level of resolution in the basal part (Fig. 6).

*Calenia* s. str. (chiefly crystalline thallus, acute or bristle-shaped hyphophores with moniliform diahyphae) forms a paraphyletic grade. No meaningful groups can be distinguished; the only clades consisting of more than two taxa belong to the *Bullatina aspidota* group (muriform ascospores, partly placodioid-bullate thallus), which is here resolved into two clades.

The *Calenia inconspicua* group and *Caleniopsis* are strongly supported as monophyletic groups in an intermediate position between *Calenia* s. str. and *Aulaxina*. The latter is also well-supported as a monophyletic group, although the sister group relationship with *Caleniopsis*, as evident from the first tree (Fig. 1), remains unresolved. *Caleniopsis* also includes the two species *Calenia conspersa* and *C. aggregata*, which have the same thallus structure (thick white thallus with dark prothallus) but lack hyphophores. No further subdivision is indicated in *Aulaxina*, except for the weakly supported monophyletic *Aulaxina minuta* group (species with dark prothallus and small apothecia).

## Distribution of major apomorphies

The foliicolous growth habit appears to have evolved more than once. Two transitions can be found within the *Gyalideopsis-Gomphillus* grade (Fig. 4): a minor one towards the somewhat isolated *G. minutissima* group, and a major one towards the *G. verruculosa* group, which includes at least one major foliicolous lineage of the family (the *Tricharia-Echinoplaca* grade; Fig. 1). A third transition is indicated by the *Gyalectidium-Actinoplaca* grade (Fig. 1); this might include the *Calenia-Aulaxina* grade (Fig. 2), although in the main tree (Fig. 1), this clade seems to be connected to the *Tricharia-Echinoplaca* grade.

If one assumes long-branch attraction due to derived, converging hyphophore features as the reason for the formation of the *Gyalectidium-Actinoplaca* grade (Fig. 1), then the *Calenia-Gyalectidium* clade in the analysis after deletion of hyphophore characters (Fig. 2) is the most likely scenario for a single origin of truly zeorine, erumpent apothecia. Immersed apothecia with a thalline rim are also known from *Diploschistella*, but their different anatomy indicates convergence rather that synapomorphy (Fig. 2).

The formation of sterile thallus setae is primarily restricted to foliicolous taxa; black

FIG. 5. Majority rule consensus of 400 equally parsimonious trees (1431 steps) including 93 taxa of the *Tricharia-Echinoplaca* grade with complete character set (140 parsimony informative characters; CI=0·24). Black/ringed/white dots indicate high (>90%), medium (70–90%), and low (50–70%) average Bootstrap/Jackknife support respectively.

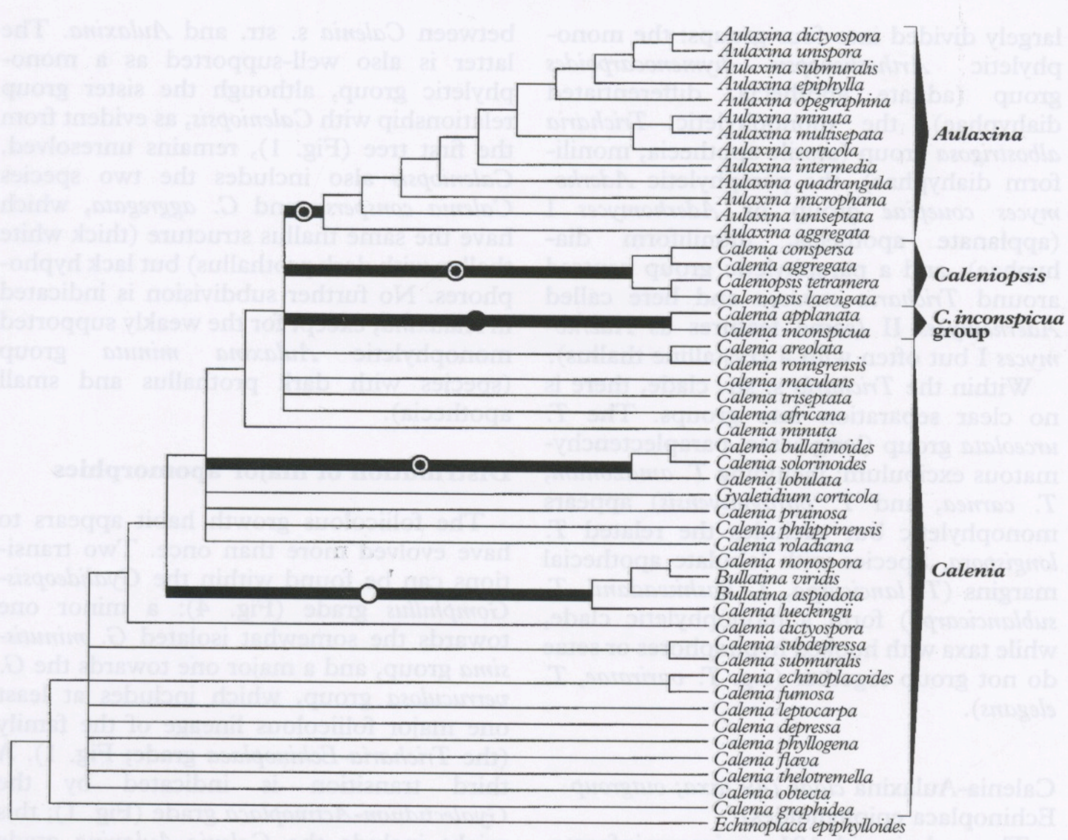



FIG. 6. Strict consensus of 16 equally parsimonious trees (632 steps) including 49 taxa of the *Calenia-Aulaxina* clade with complete character set (101 parsimony informative characters; CI=0·47). Black/ringed/white dots indicate high (>90%), medium (70–90%), and low (50–70%) average Bootstrap/Jackknife support respectively.

setae seem to have evolved twice in *Tricharia* s. str. and *Paratricharia* (Figs 1 & 2), if apothecial features are taken into consideration (compare with Fig. 3). White setae might either have evolved several times in different groups, or once with several subsequent losses (e.g. in *Aderkomyces*, *Arthotheliopsis*, *Echinoplaca* and *Calenia*; Figs 1–3).

As already mentioned, taxa with highly derived hyphophores cluster in a single clade probably because of long-branch attraction (Fig. 1); however, *Gyalectidium*, with particularly squamiform hyphophores, remains monophyletic even if hyphophores are excluded from the analysis (Fig. 2). The *Actinoplaca strigulacea* and *Gyalideopsis anastomosans* groups are clearly held together by their hyphophore types (Fig. 1), but dissolve when hyphophores are excluded (Fig. 2). In both groups, the hyphophores functionally resemble isidia, albeit representing two different evolutionary strategies: in *Actinoplaca*, the isidioid hyphophores are formed by stipeless diahyphal bunches, while in the *Gyalideopsis anastomosans* group, they show a more complex structure in which elements of the original stipe are included ('thlasidia').

## Discussion

### Character coding and data analysis

Binary coding is used less frequently than multistate coding of phenotype characters; yet, it has a number of advantages (Wiley *et al.* 1991; Poe & Wiens 2000). Multistate characters are often ill-defined, assuming that they represent states of a single character, while in fact several characters are mixed in such a definition. For example, colours or number of septa are commonly defined as states in a multistate character. However, colours might have different causes, such as the presence and density of pigments or physical attributes. Therefore, binary coding of the presence/absence of individual colour elements is more accurate than multistate coding, especially if the exact cause of the colour is known. The same is true of most other characters, for example instead of defining the number of septa as a multistate character, one could argue that each septum is an individual character, and its presence/absence is the actual state.

Binary coding also accommodates variation of character states within an operational unit. If a character is defined as multistate (such as white-yellow-red-brown-black=0-1-2-3-4), a single state has to be selected for any given operation unit (e.g. red=2), even if variation (red-brown) can be observed in that unit. With binary coding, this variation can be coded without problems (white; absent; yellow: absent; red: present; brown: present; black: absent=0/0/1/1/0). This advantage of binary over multistate coding also allows merging of operational units without losing information on their variation.

Furthermore, binary coding facilitates the detailed application of weighting (or character transformation penalties) in a straightforward fashion. In multistate characters, all states receive the same proportional weight, unless complex stepmatrices are defined for a given character. Using binary coding, such arbitrary stepmatrices are avoided. For example, in a multistate character with five states (0-1-2-3-4), a weight of 2 for that character would result in doubling the step count between each state (0-2-4-6-8). If one wants to apply a penalty only to the transformation from state 2 to state 3, a stepmatrix would have to be defined instead. In binary coding, on the other hand, every 'state' would be an individual character, and one would apply the weight or penalty just to the character representing state 3 (0-1, 0-1, 0-2, 0-1, 0-1).

Character weighting, or more correctly, applying penalties to character transformations, is an important tool in phylogenetic research. The basic problem of phylogeny is the differentiation of homoplasies and synapomorphies. Ultimately, these are recognized as such only by the resulting phylogeny, and one expects the amount of synapomorphic structure in a data set to be sufficiently high to result in a reliable topography. However, in many problematic groups, homoplasies far outnumber synapomorphies, either because the number of true homoplasies is high, or because one is unable to correctly recognize and code characters due to observational limitations. For example, while ascospore septation has long been thought to delimit larger taxonomic units, we now know that the transformation from transversely septate to muriform ascospores is a true homoplasy that occurred in a large number of taxa across the Lecanoromycetes. On the other hand, it is difficult to assess the status of characters such as colours. The same colour might have entirely different causes, unknown unless chemically traced, but recognized as potential synapomorphy by a phylogenetic algorithm.

If the amount of synapomorphic structure in the data is sufficiently high, character weighting can be applied *a posteriori* based on the distribution of characters in the tree. This will result in a more stable tree topology and higher bootstrap / Jackknife support (if the latter is done proportional to character weights). However, if there is a very high amount of homoplasy in the data, *a posteriori* character weighting can lead to biased tree topologies, because the initial tree might already be biased by homoplasies that were not recognized as such. For example, in the present case, a run with the entire data set (228 taxa, 209 characters, unweighted) resulted in a tree with an extremely low consistency index of CI=0·12, which indicates little synapomorphic structure in the data. In this case, it is more appropriate to weight characters *a priori*, based on sufficiently objective criteria such as the following:

1 Amount of variation in closely related taxa, such as ascospore septation. For example, sporomorphs, i.e. closely related species with identical morphology but different ascospore septation, are common in *Ostropales*; hence, ascospore septation usually does not give a good phylogenetic signal and has to be downweighted against certain other characters.

2 Systematic importance in related groups of lichenized fungi (*Asterothyriaceae*, *Graphidaceae*, *Thelotremataceae*). For example, in several critical revisions of Ostropalean fungi and lichens, it has been shown that excipular structure is important for delimiting genera (Sherwood 1977; Hale 1980; Staiger 2002). Hence, character states pertaining to excipular structure were assigned a higher weight in the present analysis.

3 Correlation of functionally unrelated characters among taxa (e.g. colour of setae *versus* excipulum structure). It is often postulated that characters have to be uncorrelated to be phylogenetically important (e.g. Rambold & Hagedorn 1998). However, if all characters were uncorrelated, there would be no phylogenetic signal at all. Instead, one has to distinguish between different types of correlations to assess their phylogenetic information content, i.e. correlation by definition, functional correlation, and evolutionary correlation. Obviously, defining the same character twice, for example such as carbonization of proper margin and pigmentation of excipulum, or as orange colour and presence of anthraquinones, is phylogenetically redundant and must by all means be avoided. Functional correlation, such as number of ascospores per ascus and ascospore size, has little information content (albeit greater than zero) in phylogenetic terms, but since functional correlation cannot be avoided in phenotype character coding, such characters should be downweighted against others. Evolutionary correlation, on the other hand, is phylogenetically significant, since it denotes shared synapomorphies that characterize monophyletic clades derived from a single ancestor which exhibited the correlated character states. Of course, the latter can only be assumed if functionally uncorrelated characters are involved, such as colour of thallus setae *versus* excipulum structure. Such characters (e.g. black setae *versus* paraplectenchymatous excipulum) were given a higher weighting in the present analysis.

## Genus delimitation within *Gomphillaceae*

*Actinoplaca*

This monospecific genus was established by Müller Argoviensis (1890) to accommodate *A. strigulacea*, a species characterized by the formation of globose 'sporodochia'. These 'sporodochia' are in fact hyphophores, indeed they were the first to be described, although not recognized as such. Because of its adnate apothecia, *A. strigulacea* was included in *Echinoplaca* by Santesson (1952), but Vězda & Poelt (1987) reinstated *Actinoplaca* and transferred a second species, *A. vulgaris*, to this genus, based on *Tricharia vulgaris*. This species was later recombined as *Gyalideopsis vulgaris* (Lücking 1997).

Our analysis demonstrates *Actinoplaca sensu* Vězda & Poelt (1987) to be polyphyletic: the placement of *A. vulgaris* in the genus *Gyalideopsis* is confirmed, while *Actinoplaca strigulacea* forms a highly supported clade with *Echinoplaca gemmifera*. Both share a derived, isidia-like hyphophore type, while their thalli and apothecia are *Echinoplaca*-like. The placement of this clade remains unclear. Its closeness to *Gyalectidium*, and that of other genera included in the *Gyalectidium-Actinoplaca* clade, might be a case of long branch attraction, since these taxa have strongly derived hyphophores lacking a stipe, and hence agree in that the inapplicable characters relating to stipe morphology are being treated as states with zero distances. In other words, their hyphophores apparently are convergences wrongly recognized as synapomorphies by the phylogenetic algorithm. The adnate apothecia, as well as the diahyphae, indicate a relationship with *Echinoplaca*, but since *Actinoplaca* falls outside this genus, even if hyphophore characters are deleted from the analysis, we retain *Actinoplaca* as a distinct genus and transfer into it *Echinoplaca gemmifera* even though this changes the concept of this genus as circumscribed by Vězda & Poelt (1987).

*Aderkomyces*

The originally monospecific *Aderkomyces* was established by Batista (1961) to include a species with flabelliform hyphophores, later transferred to *Tricharia* as *T. couepiae* (Lücking *et al.* 1998). The genus is here resurrected to accommodate species of *Tricharia* s. lat. with white setae, often applanate apothecia with hyphal excipulum, and partly flabellate hyphophores. The core group (*Aderkomyces* s. str.) is centred around the type species *A. couepiae* and also includes *Tricharia heterella*, of which *Psathyromyces rosacearum* is a synonym (Lücking *et al.* 1998). These species typically have a smooth thallus, large applanate apothecia and flabelliform hyphophores. A second group centred around *T. cubana* and *T. guatemalensis* is characterized by small sessile, dark apothecia with almost prosoplectenchymatous excipula. The third group includes *Tricharia albostrigosa* and relatives, characterized by sessile, light-coloured apothecia with hyphal excipula. The exact affinities of the remaining species, centred around *Tricharia cretacea*, remain obscure, mostly because hyphophores and/or diahyphae are unknown. Their thalli are typically verrucose and either corticolous or foliicolous, and their hyphophores, as far as is known, are acute-setiform.

*Arthotheliopsis*

Vainio (1896) described this originally monospecific genus for a species which he erroneously thought close to *Arthothelium* in the Arthoniomycetes. The type was later included as a synonym of *Echinoplaca heterella* (Santesson 1952), before Lücking (1997) established its validity as an autonomous species. In our analysis, *Arthotheliopsis* forms a group of five taxa, which are similar to *Aderkomyces* (white setae, non-crystalline thallus, hyphal excipulum) but differ in their adnate, *Echinoplaca*-like apothecia and their slightly differentiated diahyphae. In the general tree, these five taxa group with *Echinoplaca*, while in the more detailed *Echinoplaca-Tricharia* grade tree, they form part of *Aderkomyces*. Since there are differences from both genera, we resurrect the genus *Arthotheliopsis* for the five species included here. *Phallomyces* might be a synonym of *Arthotheliopsis*; it shares thallus, hyphophore morphology and anatomy with *A. hymenocarpoides*, but since apothecia are unknown in the type material of *Phallomyces palmae*, its position remains unclear (see Lücking *et al.* 1998).

*Aulaxina*

This genus, first included in *Gomphillaceae* by Vězda (1979), is strongly supported in our analysis; it always forms a monophyletic clade and is well defined by several apomorphies, including the carbonized zeorine apothecia and the black hyphophores with palmate diahyphae produced on an algal-free prothallus. Also, the previous assumption that *Aulaxina* is closely related to *Caleniopsis* (Vězda & Poelt 1987; Lücking 1997), and that the latter forms an evolutionary link between *Calenia* and *Aulaxina*, is confirmed by our data. The phylogenetic relationship of *Aulaxina* with *Caleniopsis* also supports the assumption that the carbonaceous margin is secondarily derived from a thalline margin, rather than representing a proper excipulum (Lücking 1997). Indeed, apothecial sections demonstrate the presence of a reduced, colourless proper excipulum in *Aulaxina*, a structure which is not found in taxa with superficially similar but genuinely lecideine apothecia, such as *Tricharia aulaxiniformis* (Lücking & Kalb 2000). This and other species of *Tricharia* with aulaxinoid apothecia, such as *T. aulaxinoides*, lack any phylogenetic relationships with *Aulaxina* in our analysis.

Subgeneric delimitation in *Aulaxina* is difficult because of homogeneity within the genus and the obvious lack of correlation between morphological (prothallus, apothecial outline) and anatomical features (ascospore septation). The tree does support the species with a dark prothallus (*A. minuta* group) as a monophyletic clade, while elongate-lirellate apothecia (*A. epiphylla*, *A. opegraphina*, *A. unispora*) seem to represent a homoplasy.

*Bullatina*

Vězda & Poelt (1987) established this originally monospecific genus to accommodate *Calenia aspidota*, a widespread and common taxon typically found on leaves in exposed situations (Lücking 2001). *Bullatina aspidota* is characterized by its strongly crystalline, bullate thallus with cellular cortex, deeply immersed apothecia with epithecial algae, muriform ascospores, and setiform, acute hyphophores with subapically inserted diahyphal bunches. However, immersed apothecia with single-spored asci producing muriform ascospores and with epithecial algae are also known in *Calenia monospora* and *C. lueckingii* (Vězda 1979; Hartmann 1996), and the hyphophores of *Bullatina* are essentially identical with those of *Calenia* s. str. and *Echinoplaca epiphylla* (Lücking 1997). Hence, the only remaining diagnostic character separating *Bullatina* from *Calenia* was the bullate thallus with a cellular cortex. Yet, this delimitation was obscured by Brusse (1992, 1993), who included two further species in that genus, viz. *Bullatina microcarpa* and *Bullatina viridis*, both lacking the thallus morphology characteristic of *B. aspidota*. *Bullatina microcarpa* was recently transferred to *Gyalectidium* (Ferraro *et al.* 2001), whereas *Bullatina viridis* is most probably a synonym of *Calenia monospora*.

The remaining species, *Bullatina aspidota*, merges with *Calenia* in our analysis, and the species indeed features most of the characters typical of the latter (zeorine apothecia, acute hyphophores with moniliform diahyphae). Since some species of *Calenia* do have a slightly bullate thallus (*C. solorinoides*, *C. bullatinoides*), there is no reason to keep *Bullatina aspidota* in a separate genus. The bullate thallus and the cellular cortex are considered ecomorphological adaptations to high light intensities (Lücking 2001), and as such of no systematic value at generic level when found only in a single taxon. There is also no support for a larger *Bullatina* clade that would include *Calenia solorinoides* and *C. bullatinoides*, since these species do not differ significantly from *Calenia* s. str. *Bullatina* thus becomes a synonym of *Calenia*, and the previous name *Calenia aspidota* is resurrected here.

*Calenia*

Contrary to our previous expectations, the bulk of *Calenia* forms a coherent, though paraphyletic group in our analysis, although infrageneric resolution is low. Three species are here excluded from this genus: *Calenia conspersa* and *C. aggregata* are transferred to *Caleniopsis*, with which they share the same thallus and apothecial morphology. *Calenia inconspicua* is distinct in having immersed, applanate, translucent apothecia, and always falls close to the *Aulaxina*/*Caleniopsis* clade. For this species, we describe the new genus *Aplanocalenia*.

The remaining species of *Calenia* are characterized by immersed-erumpent apothecia with non-carbonized margin, mostly verrucose thalli incrusted with crystals (rarely smooth and lacking crystals), and laminal, acute- or blunt-setiform hyphophores producing undifferentiated diahyphae. The assumption that *Calenia* is derived from *Echinoplaca* (Lücking 1997), via secondary formation of a thalline margin from adnate, emarginate apothecia, is supported by our analysis.

There is some indication that *Calenia* can be divided into three major groups: the *Calenia depressa* group, with mostly medium-sized, vermiform ascospores and acute hyphophores; the *C. bullatinoides* group, with muriform ascospores and mostly blunt hyphophores and often strongly crystalline thalli, and the *C. triseptata* group, with small, mostly 3-septate ascospores and lacking hyphophores. However, these groups are not supported, and the placement of most species with lobulate apothecial margins and lacking hyphophores remains unclear.

*Caleniopsis*

The establishment of *Caleniopsis* as a taxon distinct from *Calenia* and related to *Aulaxina* (Vězda & Poelt 1987; Lücking 1997) is clearly supported by our analysis. *Caleniopsis* and *Aulaxina* share the same hyphophore type, but the latter differs in the carbonized apothecial margin. Two further species of *Calenia*, viz. *C. conspersa* and *C. aggregata*, fall into this group and are here transferred to *Caleniopsis*. Hyphophores are unknown in both taxa, but their aspect, especially of *C. conspersa*, is very similar to that of *Caleniopsis laevigata*. All four species have thalli encrusted with calcium oxalate crystals, but unlike *Calenia* s. str., which is verrucose, possess a smooth, whitish surface. In addition, all species have small, 1–7-septate ascospores, and *Caleniopsis laevigata*, *Calenia conspersa* and *C. aggregata* share a dark prothallus.

*Diploschistella*

The resurrected genus *Diploschistella* includes four saxicolous or terricolous species previously placed in *Gyalideopsis* but with immersed apothecia. Incomplete hyphophore data are available for one species, *D. lithophila*, but it is uncertain whether the hyphophores really belong to that species.

*Echinoplaca*

Quite unexpectedly, this genus is rather coherent in our analysis, though apparently paraphyletic. The only group that is somewhat outside the typical variation of *Echinoplaca* is the *Arthotheliopsis hymenocarpoides* group, which has smooth thalli lacking crystals, and which is here resurrected as *Arthotheliopsis*. *Echinoplaca* s. str. is uniformly characterized by adnate apothecia and a verrucose thallus incrusted with crystals. The hyphophores, as far as is known, are mostly of a plesiomorphic type, being acute- to blunt-setiform. The genus includes a number of rather distinct groups, all characterized by a certain combination of thallus, apothecial, and hyphophore features, but the lack of hyphophores in many species makes a clear subdivision of *Echinoplaca* difficult at present. However, it can be stated that this genus includes several excellent examples of sporomorphs, i.e. species or series of species that differ only in their ascospore septation: the *E. leucotrichoides* group (of which *Sporocybomyces* is a synonym), which possibly also includes *E. macgregorii* (hyphophores unknown), i.e. species with ascospores ranging from small 5-septate, to vermiform multiseptate, to large muriform; the *E. lucernifera* group, which also includes *E. tetrapla* (hyphophores unknown) and thus a series of taxa ranging from small 5-septate to large muriform ascospores; the *E. furcata* group (small submuriform to large muriform); the *E. atrofusca* aggregate (vermiform multiseptate to large muriform); and the *E. diffluens* aggregate (vermiform multiseptate to large muriform).

*Gomphillus*

The three species of *Gomphillus* appear as a well-defined, monophyletic clade nested within *Gyalideopsis*, but clearly separated from the latter by the vertically elongate apothecia with very long asci and filiform-acicular ascospores. The umbellate hyphophores found in *G. americanus* resemble those of *Gyalideopsis lambinonii* and *G. japonicum*, but differ in their very long stipe. Because of the distinctive apothecial and hyphophore features, *Gomphillus* is retained as a separate genus.

*Gyalectidium*

This genus forms a highly supported monophyletic clade, characterized by strongly derived, squamiform hyphophores, in combination with *Calenia*-type apothecia. It was already treated in much detail in the recent monograph of Ferraro *et al.* (2001), and several further species have been described since then (Herrera-Campos & Lücking 2002, 2003; Lücking *et al.* 2003;

Ferraro & Lücking 2003; Herrera-Campos *et al.* 2004).

*Gyalideopsis*

As assumed by previous authors (Vězda & Poelt 1987; Lücking 1997; Dennetière & Péroni 1998), *Gyalideopsis* takes a basal position in the family, if *Gyalidea* (*Asterothyriaceae*) is selected as outgroup. Owing to the large number of species so far described in this genus, and the large variation in thallus, apothecium and hyphophore characters, a case might be made to divide the genus into smaller entities. On the other hand, with a few exceptions, variation within this genus is no higher than in other presumably natural groups, such as *Aderkomyces*. Indeed, apothecia varying from sessile-stipitate to applanate or with lobulate thalline margin are also known from *Aderkomyces*. The hyphophores of most species of *Gyalideopsis* can be easily derived from a plesiomorphic setiform type, via reduction of the stipe and flattening and enlargement of the apical part, and the same kind of variation is known in *Aderkomyces*. Thus, although some groups within the genus are rich in species and indicate strong radiation, their separation at generic level is not indicated. The situation is further complicated by species in which hyphophores are unknown (including the type species), and whose generic placement would be arbitrary without knowledge of that structure.

Based on our results and after careful considerations, however, we recognize four distinct groups as separate genera. The resurrected genus *Diploschistella* includes four saxicolous or terricolous species characterized by immersed instead of sessile apothecia. The new genus *Jamesiella*, named after the distinguished British lichenologist Peter James who first discovered the type species, comprises the three taxa of the *Gyalideopsis anastomosans* group, which feature particular isidioid hyphophores ('thlasidia') unique in the family. In addition, we establish the new genus *Lithogyalideopsis* for four saxicolous species with blackish apothecia, small ascospores and *Aulaxina*-like hyphophores (the *Gyalideopsis aterrima* group), and the new genus *Ferraroa*, named after our friend and distinguished lichenologist from Argentina, Lidia Ferraro, for *Gyalideopsis hyalina*, which exhibits a very distinctive hyphophore type that resembles campylidia of the *Pilocarpaceae* (Lücking 1995; Sérusiaux 1995). Such hyphophores are otherwise unknown in the *Gomphillaceae*, although the filiform diahyphae are the same as those found in *Gomphillus* and several species of *Gyalideopsis*.

The remainder of *Gyalideopsis* can be chiefly arranged into four major groups, which are not formally recognized because of the lack of hyphophore data for many species: the *G. africana* group, which is characterized by setiform-capitate hyphophores and an often muscicolous growth habit. This group is likely to include the type species of the genus, *G. peruviana*, in which hyphophores are so far unknown, and the type species of *Microlychnus* (already recombined as *Gyalideopsis* by Tønsberg in Vězda 2003). At present, we also include the saxicolous species lacking hyphophores in this group.

The second group, centred around *G. palmata*, includes mostly corticolous taxa with flabelliform hyphophores. Our data does not support the assumption that species with filiform (including the type species of *Epilithia*) or moniliform diahyphae (including the type species of *Microspatha*) each form distinct groups, but this aspect should be studied in more detail when molecular data are available.

The other two groups chiefly comprise the foliicolous representatives of the genus. In our analysis, they seem to represent two distinct entities: one group centred around *Gyalideopsis minutissima*, with mostly small apothecia and ascospores and either unknown or strongly derived hyphophores and partly with a lichenicolous habit; and the other, including *G. verruculosa* and relatives, with usually crystalline thalli, rather short, setiform hyphophores producing moniliform diahyphae, and a strong tendency to produce muriform ascospores.

*Hippocrepidea*

The genus *Hippocrepidea* was established by Sérusiaux (in Aptroot *et al.* 1997) to accommodate the single species *H. nigra*. This taxon has apothecia similar to those of *Gyalideopsis*, but its hyphophores and diahyphae are highly derived, the hyphophores being visible as crescent-shaped scales adnate to the thallus. The situation of *Hippocrepidea nigra* can thus be compared to *Gyalideopsis hyalina*, but contrary to the latter, *Hippocrepidea nigra* also features a particular type of branched diahyphae unique within the family. We therefore retain this taxon at generic level.

*Paratricharia*

Like *Hippocrepidea*, *Paratricharia* is a monospecific taxon. *Paratricharia paradoxa* is very distinctive because of its black-setose thallus and its *Aulaxina*-like apothecia with a central columella (Lücking 1991, 1997). This combination of features, as well as the formation of a columella, is unique within the family and justifies the recognition of the species at generic level. Although *P. paradoxa* seems to be close to *Aulaxina*, its relationships remain obscure, since this may be a case of long branch attraction due to the very derived apothecia shared by both genera.

*Tricharia*

Besides *Gyalideopsis*, *Tricharia* in its present sense is the most heterogeneous entity within the *Gomphillaceae*, and this view is confirmed by our analysis. Indeed, *Tricharia* can be divided into three groups which are well characterized by a combination of functionally unrelated characters: the *Aderkomyces couepiae* group, with mostly non-crystalline thalli, white setae, sessile to applanate apothecia with mostly hyphal excipula, and white to apically darkened, stipitate and apically often widened hyphophores; the *Tricharia helminthospora* group, with non-crystalline thalli, dark reddish brown setae with pale tips, sessile to almost stipitate apothecia with hyphal excipula, and hyphophores similar to those of the *Aderkomyces couepiae* group; and *Tricharia* s. str., with often crystalline thalli, black setae, sessile to almost stipitate apothecia with proso- to paraplectenchymatous excipula, and black, mostly setiform hyphophores. Considering the number of differences between the species with white and with black setae, and the fact that they separate in our analyses, we resurrect the genus *Aderkomyces* to accommodate the former group, and establish the new genus *Rubrotricha* for the *Tricharia helminthospora* group.

Subdivisions within *Tricharia* s. str. are difficult at present, although most species can be assigned to two distinct groups. The first group is characterized by smooth thalli lacking crystals, rather short setae, and a typically prosoplectenchymatous excipulum. It comprises the *T. vainioi* group, with setiform hyphophores, and the *T. elegans* group, with umbellate-hooked hyphophores and/or setae. The second group, centred around the lectotype species *T. urceolata*, comprises species with mostly verrucose thalli and rather long setae, and typically paraplectenchymatous exciple. The placement of the remaining species, such as *T. cuneata* with flabelliform hyphophores and a smooth thallus, and *T. farinosa*, with blunt-setiform hyphophores, a verrucose thallus usually provided with a dark prothallus, and brown, often farinose, flat apothecia with a prosoplectenchymatous excipulum, remains obscure.

The only species which seems to fall outside the typical variation found in *Tricharia* s. str. is *Tricharia aulaxinoides*. It has two features that are unique as compared to the other species: apothecial margins covered by thin black thalline lobules, and the apical differentiation of its diahyphae. *Tricharia brevipilosa* is one of two taxa now considered to belong in *Gyalideopsis*, since its setae seem to be postmature hyphophores. The available material of *Tricharia vezdae* strongly suggests that the few 'sterile' black setae are in fact postmature or broken hyphophores, and indeed, other features clearly place this taxon within *Gyalideopsis*, where it is retained under the new name *G. buckei* (since *G. vezdae* already exists).

TABLE 3. *Synopsis of currently recognized genera in the lichen family* Gomphillaceae. *Species numbers include some new species to be described in forthcoming publications. Characters in paraentheses indicate the character to be present in some species of the genus*

| Genus | Synonym(s) | Species | Setae | Apothecia | Hyphophores | Diahyphae |
|---|---|---|---|---|---|---|
| *Actinoplaca* | | 2 | absent | adnate | isidioid | derived |
| *Aderkomyces* | *Psathyromyces* | 25 | (white) | applanate-sessile | setif.-flabellate | moniliform |
| *Aplanocalenia* | | 2 | absent | immersed | unknown | unknown |
| *Arthotheliopsis* | *Phallomyces* | 5 | (white) | adnate | setif.-flabellate | apically moniliform |
| *Aulaxina* | *Lochomyces* | 13 | absent | erumpent-carbonized | setiform | palmate |
| *Calenia* | *Bullatina, Phlyctidium* | 29 | (white) | erumpent-zeorine | setiform | moniliform |
| *Caleniopsis* | | 4 | (red-brown) | erumpent-zeorine | setiform | palmate |
| *Diploschistella* | | 4 | absent | immersed | (unknown) | (unknown) |
| *Echinoplaca* | *Spinomyces, Sporocybomyces* | 32 | (white) | adnate | setiform | monilif.-derived |
| *Ferraroa* | | 1 | absent | sessile | campylidioid | filiform |
| *Gomphillus* | | 4 | absent | elongate | umbellate | filiform |
| *Gyalectidium* | *Gonothecium, Lopadiopsis, Tauromyces* | 41 | (white) | erumpent-zeorine | squamiform | moniliform |
| *Gyalideopsis* | | 82 | absent | applanate-sessile | setif.-flabellate | filiform-moniliform |
| *Hippocrepidea* | | 1 | absent | applanate-sessile | lunulate | branched |
| *Jamesiella* | | 4 | absent | applanate-sessile | isidioid ('thlasidia') | compact |
| *Lithogyalideopsis* | | 4 | absent | sessile | setiform | palmate |
| *Paratricharia* | | 1 | black | erumpent-carbonized | unknown | unknown |
| *Rubrotricha* | | 2 | red-brown | sessile | setif.-flabellate | moniliform |
| *Tricharia* | *Microxyphiomyces, Setomyces* | 26 | black | sessile | setiform | moniliform |

**Key to genera and subgeneric entities of *Gomphillaceae***

The following key distinguishes the generic and subgeneric entities now recognized within the *Gomphillaceae* (Table 3):

1 Apothecia adnate to sessile or shortly stipitate or vertically elongated, with well-developed or reduced proper excipulum but lacking algiferous thalline margin, rarely with thin thalline lobes laterally covering excipulum . . . . . 2

Apothecia immersed-erumpent, with well-developed, algiferous thalline margin or with carbonized thalline margin, proper excipulum reduced . . . . . . . . 13

2(1) Apothecia vertically elongate; ascospores filiform-acicular; hyphophores unknown or umbellate with long stipe . . . . . **Gomphillus**

Apothecia not vertically elongate; ascospores oblong-ellipsoid to ovoid; hyphophores not as above, if umbellate then with short stipe . . . . . . . . . . 3

3(2) Thallus with black setae; apothecia sessile to stipitate; excipulum proso- or paraplectenchymatous . . . . . . . . . . **Tricharia**

Thallus lacking sterile setae or with white to reddish brown setae; apothecia sessile to applanate or adnate; excipulum typically hyphal, rarely proso- or paraplectenchymatous . . . . . 4

4(3) Hyphophores crescent-shaped, adnate to thallus; diahyphae branched from single point, with non-septate segments **Hippocrepidea**

Hyphophores setiform to flabelliform or umbelliform, rarely campylidiiform or isidiiform; diahyphae not as above, usually filiform or moniliform . . . . . . 5

5(4) Apothecia adnate, with evanescent margin and proper excipulum spreading over thallus surface . . . . . . . . . . . . 6

Apothecia applanate to sessile or stipitate, with permanent or evanescent margin and proper excipulum not spreading over thallus surface . . . . . . . . . . . 8

6(5) Hyphophores adnate, globose or disc-shaped, isidioid . . . . . . **Actinoplaca**

Hyphophores setiform . . . . . . . . . . . . . . 7

7(6) Thallus lacking calcium crystals, smooth; hyphophores setiform or flabellate; diahyphae apically moniliform, basally usually filiform **Arthotheliopsis**

Thallus with calcium oxalate crystals, usually verrucose; hyphophores setiform; diahyphae variously shaped, often strongly differentiated apically . . . . . . . . **Echinoplaca**

8(5) Setae present; thallus mostly foliicolous and then lacking calcium crystals, smooth or rarely papillose . . . . . . . . . 9

Setae absent; thallus on various substrata, if foliicolous, then mostly verrucose owing to incrustation with calcium oxalate crystals . . . . . 10

9(8) Setae reddish brown, with pale tips . . . . . . . . **Rubrotricha**

Setae white **Aderkomyces**

10(8) Hyphophores isidioid ('thlasidia'), with diahyphae together with algal cells enclosed in stipe . . . . . . . . . . **Jamesiella**

Hyphophores setiform to flabelliform or palmate, rarely umbelliform or campylidiiform, producing filiform or moniliform diahyphae . . . . . . . . 11

11(10) Hyphophores campylidiiform **Ferraroa**

Hyphophores setiform to flabelliform or palmate, rarely umbelliform. . . . . 12

12(11) Hyphophores setiform, black, with palmate diahyphae (moniliform with hyphal cord) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Lithoyalideopsis**
Hyphophores setiform to flabelliform, rarely umbelliform, with filiform or moniliform diahyphae lacking hyphal cord . . . . . . . . . . . . . . . . . **Gyalideopsis**

13(1) Apothecial (thalline) margin carbonized, dark brown to black . . . . . 14
Apothecial (thalline) margin not carbonized, whitish to pale greenish grey . . 15

14(13) Thallus with long black setae; apothecia with central, dark columella . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Paratricharia**
Thallus lacking setae but short black hyphophores usually present on translucent to blackish prothallus; apothecia lacking columella . . . . . . . . . **Aulaxina**

15(13) Hyphophores typically squamiform, with scales emerging from diahyphal mass adnate to thallus; scale sometimes divided into groups of setae; excipulum often separated from thallus margin by fissure in old apothecia; ascospores 1 per ascus, muriform (*Gyalectidium*) . . . . . . . . . . . . . . . . . . . . . . . . . . 16
Hyphophores setiform, with diahyphae produced in a bunch at or near tip, or hyphophores unknown; excipulum usually not separated from thalline margin; ascospores 1–8 per ascus, transversely septate to muriform . . . . . . . . 20

16(15) Diahyphal mass raised over thallus surface and enclosed in circle of narrowly squamiform hyphophore scales resembling a goniocystangium; diahyphal cells almost globose, outer cells forming long cilia in mature condition . . . . . . . . . . . . . . . . . . . . . . . . **Gyalectidium sect. Goniolectidium**
Diahyphal mass adnate or rarely somewhat raised; hyphophore scales squamiform or divided into groups of cilia; diahyphal cells sausage-shaped . . . . . 17

17(16) Thallus with setae, coarsely verrucose; hyphophores unknown . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Gyalectidium sect. Setolectidium**
Thallus lacking setae or rarely with setae and then smooth; hyphophores usually present . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 18

18(17) Thallus finely verrucose . . . . . . . . **Gyalectidium sect. Gyalectidium**
Thallus smooth to areolate or placoid due to large clusters of calcium oxalate crystals . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 19

19(18) Thallus smooth or areolate, with crystalline areoles separated by thin, greenish thallus areas . . . . . . . . . . . . . . **Gyalectidium sect. Areolectidium**
Thallus placoid to almost bullate, nearly completely incrusted with crystalline clusters . . . . . . . . . . . . . . **Gyalectidium sect. Placolectidium**

20(15) Apothecial margin thin to almost absent, hardly raised over thallus level; apothecial disc translucent; thallus lacking crystals, smooth, pale greenish grey . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Aplanocalenia**
Apothecial margin well-developed, if thin and hardly raised over thallus level then apothecial disc yellowish brown and thallus finely verrucose, or thallus on inorganic substrata . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 21

21(20) Apothecia with well-developed proper margin, but immersed with thalline rim; on inorganic substrata . . . . . . . . . . . . . . . . . . . . . . . . . **Diploschistella**
Apothecia with strongly reduced proper margin and dominant thalline margin; usually foliicolous . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 22

22(21) Hyphophores formed on translucent to dark prothallus, palmate; diahyphae usually with long hyphal cords; thallus encrusted with crystals forming continuous layer, thallus therefore smooth, yellowish white . . . . . **Caleniopsis**
Hyphophores formed on or at margin of algiferous thallus, diahyphae undifferentiated; thallus usually incrusted with crystals and finely verrucose, rarely smooth and lacking crystals, green to greenish grey . . . . . . . . . . . **Calenia**

## Phylogenetic relationships within *Gomphillaceae*

Our study supports the recognition of the following 19 genera within *Gomphillaceae* (in systematic order): *Diploschistella*, *Lithogyalideopsis*, *Gyalideopsis*, *Jamesiella*, *Gomphillus*, *Ferraroa*, *Hippocrepidea*, *Tricharia*, *Rubrotricha*, *Aderkomyces*, *Arthotheliopsis*, *Echinoplaca*, *Actinoplaca*, *Calenia*, *Aplanocalenia*, *Caleniopsis*, *Aulaxina*, *Paratricharia*, and *Gyalectidium*. Our analysis does not present enough resolution and support to arrange these genera into formal infrafamiliar taxa, but based on their presumed interrelationships they can be arranged into two groups.

The *Gyalideopsis* group forms the basal lineage and includes all genera with mostly sessile to adnate, rarely immersed, usually biatorine or lecideine apothecia, and with mostly stipitate, often flabelliform hyphophores: *Diploschistella*, *Lithogyalideopsis*, *Gyalideopsis*, *Jamesiella*, *Gomphillus*, *Ferraroa*, *Hippocrepidea*, *Tricharia*, *Rubrotricha*, *Aderkomyces*, *Arthotheliopsis*, *Echinoplaca*, *Actinoplaca*. This group could be further divided into the chiefly non-foliicolous and foliicolous-montane genera (*Diploschistella*, *Lithogyalideopsis*, *Gyalideopsis*, *Jamesiella*, *Gomphillus*, *Ferraroa*, *Hippocrepidea*) and the chiefly foliicolous and tropical genera (*Tricharia*, *Rubrotricha*, *Aderkomyces*, *Arthotheliopsis*, *Echinoplaca*, *Actinoplaca*). *Gomphillus*, with its vertically elongate apothecia and filiform ascospores, represents an evolutionary trend unique within the family. Nevertheless, our analysis and other features of *Gomphillus* clearly suggest a *Gyalideopsis*-like ancestor similar to *G. muscicola*.

The second lineage is comprised of mostly foliicolous taxa with typically zeorine apothecia: *Aplanocalenia*, *Calenia*, *Caleniopsis*, *Aulaxina*, *Paratricharia*, and *Gyalectidium*. Hyphophores vary strongly in this group, and we cannot exclude that this group is actually polyphyletic, with *Gyalectidium* and squamiform hyphophores having evolved independently. However, since there is no other taxon indicated as ancestral to the squamiform hyphophore type, and the position of *Gyalectidium* in the tree could therefore be due to long branch attraction, its placement near *Calenia*, which has essentially the same apothecial type, seems the best solution at present.

## Character evolution within *Gomphillaceae*

### *Ecology*

The *Gomphillaceae* are quite a variable group regarding their biological nature and substratum preferences. Four species are lichenicolous: one is found in *Aulaxina* (Lücking & Kalb 2002), and the three others belong to *Gyalideopsis* (Lücking 1997; Lücking & Sérusiaux 1998); they produce apothecia and hyphophores typically found in these genera. All other species are lichenized, and other studies indicate that the ancestral condition is the lichenized state, i.e. the lichenicolous taxa are considered to be secondarily delichenized. Interestingly, three of the four lichenicolous species occur on other *Gomphillaceae*, i.e. they are adelphoparasitic, while one grows on *Pilocarpaceae* (Lücking 1997).

The enormous radiation within the family is clearly related to the evolution of the foliicolous growth habit. Of the 19 genera, four are essentially non-foliicolous (*Diploschistella*, *Jamesiella*, *Lithogyalideopsis*, *Gomphillus*; with a total of 16 species), one is mostly non-foliicolous (*Gyalideopsis*), one is mostly foliicolous (*Aderkomyces*), and the remaining 13 are almost exclusively foliicolous (*Ferraroa*, *Hippocrepidea*, *Tricharia*, *Rubrotricha*, *Arthotheliopsis*, *Echinoplaca*, *Actinoplaca*, *Calenia*, *Aplanocalenia*, *Caleniopsis*, *Aulaxina*, *Paratricharia*, *Gyalectidium*). According to our data, the main transition from a corticolous or muscicolous to a foliicolous growth habit seems to have taken place within *Gyalideopsis*, specifically between the *Gyalideopsis palmata* and *G. verruculosa* groups. This is supported by the fact that most non-foliicolous representatives of the family (*Gyalideopsis*, *Diploschistella*, *Jamesiella*), prefer temperate or tropical-montane to upper montane or even alpine habitats, while the foliicolous taxa are most diverse in lowland to lower montane environments, with the only exception being the species of the *Gyalideopsis verruculosa* group. It is unclear from the data if there has been more than one major transition towards a foliicolous growth habit, but a few genera, such as *Tricharia* and *Aderkomyces*, seem to include species with a secondary transition to corticolous growth.

*Thallus morphology and anatomy*

Thallus morphology and anatomy in the *Gomphillaceae* includes four major character complexes: incrustation of the thallus with calcium oxalate crystals, formation of thallus setae, formation of a prothallus, and formation of a cellular cortex. Incrustation of the thallus with calcium oxalate crystals is rather strongly correlated with a foliicolous growth habit and possibly represents an ecological adaptation to this enviroment (Lücking 2001). The verrucose thallus found in most foliicolous *Gomphillaceae* is very characteristic and allows identification of completely sterile specimens at family level. Therefore, while the deposition of calcium oxalate crystals in the thallus is certainly a false homoplasy that is commonly found in lichens, the particular thallus structure in the *Gomphillaceae* has to be considered either a true homoplasy or a synapomorphy with secondary loss. Although the crystalline thallus is considered an ecological adaptation, the thallus structure that results from the incrustation with crystals is mostly characteristic of smaller or larger natural entities within *Gomphillaceae*. Thus, the *Gyalideopsis verruculosa* group, the *Tricharia urceolata* group, *Echinoplaca*, *Calenia* and *Gyalectidium* typically have crystalline thalli, while those of the *Tricharia vainioi* group, *Aderkomyces* s. str., *Arthotheliopsis*, and *Aulaxina* are smooth. In *Gyalectidium*, the two larger sections differ in having either a verrucose or a placoid thallus. Thus, the presence of calcium oxalate crystals and their distribution within the thallus can indicate systematic relationships between particular groups of species.

The abundant formation of sterile setae composed of agglutinated hyphae is one of the most characteristic features in *Gomphillaceae* and, as such, unique among lichenized fungi. This feature is also correlated with the foliicolous growth habit, although it seems to have evolved later than calcium oxalate incrustation. Sterile setae are without any doubt phylogenetically derived from setiform hyphophores (Vězda 1979; Vězda & Poelt 1987; Lücking 1997), and hence cannot be compared with cilia, rhizinae or other comparable structures found in other lichens. Within the family, two main types of setae can be distinguished: whitish to reddish brown, rather flexible and often bent, and black, stiff and straight. These two types are probably not homologous but might have been derived independently from fertile hyphophores, since their colour usually corresponds to that of the hyphophores within a given group. Whitish setae are found abundantly throughout the family, for example in *Aderkomyces*, *Arthotheliopsis*, *Echinoplaca*, and *Calenia*.

Reddish brown setae are comparatively rare and found in three species within two non-related groups (*Rubrotricha*, *Caleniopsis*), while black setae are largely restricted to the genus *Tricharia* s. str. and found in only a single further taxon, *Paratricharia paradoxa*, which is not related to *Tricharia*. Thus, black setae chiefly conform to a phylogenetic homology or synapomorphy, which means that their presence strongly suggests that the taxon in question belongs in *Tricharia*.

A translucent prothallus is a rather common feature in foliicolous taxa and possibly an adaptation enabling them to adhere to the leaf surface via a layer of acid carbohydrates. A light or dark prothallus surrounding algiferous thallus patches usually denotes smaller groups of related species, such as *Tricharia farinosa* and *T. novoguineensis*, *Caleniopsis*, and the *Aulaxina minuta* group. A cartilaginous cortex formed by a thin layer of indifferent, periclinal, gelatinized hyphae is typical of most *Gomphillaceae*. A characteristic cellular cortex is developed only in *Gyalectidium* section *Gyalectidium*. This cortex therefore denotes a synapomorphy for the species of this section.

*Apothecial morphology and anatomy*

Apothecia in the *Gomphillaceae* are basically characterized by a hemiangiocarpous development i.e. young apothecia have a covering layer made of generative tissue externally covered by a thin thalline layer, such as found in *Asterothyriaceae* (Henssen & Lücking 2002). While the generative covering layer ruptures very early during ontogeny, the thalline layer is often seen as triangular lobes and sometimes even visible in mature apothecia. Variation of apothecial features in the family is based on this ontogeny and points in different directions: formation of a stipe or vertical elongation of the hymenium; horizontal elongation of the hymenium and lateral growth with reduction of the margin; and immersion into the thallus and formation of a thalline margin which eventually can be carbonized (Lücking 1997). Such a variation is not untypical within a family and is, for example, also found in other well-delimited families such as the related *Asterothyriaceae* or the *Physciaceae* and *Ramalinaceae* (Lücking 1999; Henssen & Lücking 2002).

The sessile *Gyalideopsis*-type apothecium with hyphal excipulum composed of radiating hyphae embedded in a gelatinous matrix is the most plesiomorphic type in the family and is also found in the outgroup genus *Gyalidea* (*Asterothyriaceae*). Vertically elongate apothecia, in combination with very long asci and filiform-acicular ascospores, have evolved only once and denote a synapomorphy characteristic of the genus *Gomphillus*. Stipitate apothecia evolved several times within *Gyalideopsis* and *Tricharia* and are, like vertically elongate apothecia, often related to a muscicolous growth habit or formed in connection with the presence of long setae around the apothecia, possibly to enhance ascospore dispersal. Since such apothecia are also found in other taxa outside the family but often related to muscicolous growth habit (e.g. *Calopadia turbinata*), they are considered an ecologically driven homoplasy. The same is true of the applanate to adnate apothecia commonly found in *Gyalideopsis*, *Aderkomyces*, *Arthotheliopsis*, and *Echinoplaca*, but also known from foliicolous members of other families, such as the *Arthoniaceae* or *Pilocarpaceae*.

A tendency to form immersed apothecia can be seen in several non-related taxa, such as *Diploschistella* and the *Calenia*-*Aulaxina* clade. A few species within different genera retain the thin thalline lobes originally covering the disc during apothecial ontogeny in the mature condition, such as *Gyalideopsis lobulata*, *Tricharia lancicarpa*, *Aderkomyces purulhensis*, and *Calenia obtecta*. They do not form natural entities but are closely related to species with apothecia lacking such lobes (*Gyalideopsis pallescens*, *Tricharia vainioi*, *Aderkomyces albostrigosus*, *Calenia phyllogena*). This behaviour is also known from related families such as the *Asterothyriaceae* and *Thelotremataceae*. The aforementioned apothecia of *Diploschistella* and *Calenia* are anatomically different; in the latter, the thalline margin is firmly connected to the proper margin to form zeorine apothecia. Since based on our data we assume monophyly for this lineage, this character is to be interpreted as synapomorphy. The same is true of the zeorine apothecia with carbonized margin typical of the genus *Aulaxina* (with the possible exception of *Paratricharia*).

Ascospore septation, in traditional classifications often used to distinguish genera, clearly varies even between closely related species, which supports the sporomorph concept and underlines that ascospore features should be considered with great caution when assessing phylogenetic relationships. Indeed, in our analysis, ascospore septation is by far the most homoplastic of all characters, with transitions from transversely septate to muriform ascospores occurring in almost all genera.

*Hyphophore morphology and anatomy*

Hyphophores are the most enigmatic character and the true anagenetic feature reflecting the evolution of the family. Based on our data and other studies (Sérusiaux & De Sloover 1986; Vězda & Poelt 1987; Dennetière & Péroni 1998; Ferraro 2004), setiform hyphophores with apically inserted, filiform diahyphae seem to be among the most plesiomorphic types within the family; such hyphophores are typical of several species of *Gyalideopsis* in both the *G. africana* and the *G. palmata* groups. This type seems to have evolved, partly independently, in several directions: reduction of the upper and/or lower portion of the stipe; widening of the upper portion of the stipe; inclusion of crystals in or development of a tomentum along the stipe; dark pigmentation; division of the diahyphal mass into separate entities; transition from filiform to moniliform diahyphae with constrictions at the septa; further differentiation of (terminal) diahyphal segments; and inclusion of algal cells with the diahyphae. All derived hyphophore types can be explained by a combination of these developmental features, and while some types are connected by intermediate forms, others are very distinctive. Two previously unknown, branched setiform hyphophore types have been recently described by Ferraro (2004). Since they belong to unknown taxa, we have not included them in this analysis, but they most closely fit the *Echinoplaca* and *Calenia* hyphophore types and probably do not represent unrecognized genera.

Hyphophores clearly denote an evolutionary homology, i.e. a character complex with a common ancestry that evolved via divergence into very different types. Eventually these types functionally resemble quite different dispersal structures, such as isidia and 'thlasidia' (*Actinoplaca*, *Jamesiella*), soralia (*Gyalectidium yahriae*), and even campylidia (*Ferraroa*). As such, while hyphophores diverged into very different types, they demonstrate a high degree of convergence with dispersal structures known from other lichens, indicating a strong selective pressure, especially in foliicolous taxa (Lücking 2001).

Evolutionary theory assumes that a newly invented character via anagenesis initially shows high evolutionary plasticity, while it eventually becomes stabilized at later stages. Thus, it is expected that a plesiomorphic taxon within a given group shows a higher variation in this feature than an apomorphic taxon. This pattern can indeed be observed in the *Gomphillaceae*: *Gyalideopsis* is considered rather basal and includes species with variable hyphophore types, while the strongly derived genera *Aulaxina* and *Gyalectidium* have rather uniform hyphophores.

Obviously, the invention of the new character complex represented by the hyphophores at first allowed a rather free variation and evolution into different directions, with little impact on their dispersal effectiveness. At some points, however, the resulting structures achieve functional specifications that allow selective pressure to work strongly on them and rapidly select highly derived hyphophore types. This might explain why there are hardly any intermediate types between the wide array of setiform to flabelliform or umbelliform hyphophores and the highly derived types resembling isidia, soralia, or campylidia. This might also be the reason for the phenomenon that taxa with very similar apothecial types, such as *Calenia* and *Gyalectidium*, might have very different hyphophore types. All together, the hyphophores of the *Gomphillaceae* are an excellent example for character evolution following anagenesis and the mutual effect of free variation *versus* driving forces, resulting in divergence and convergence at the same time.

## Conclusions

Phenotype data are usually affected by variation due to ontogenetic development, sexual dimorphism, and environmental factors, which means that they contain less phylogenetic structure than genotype data. Thus, the results of our phenotype-based phylogenetic analysis are of a preliminary nature, and the validity of even well-supported groups must be tested using molecular approaches, such as those initiated by Lücking *et al.* (2004).

On the other hand, the partial 'confusion' regarding generic delimitation in the *Gomphillaceae* arose from the seemingly uncorrelated variation of phenotypic characters, and it is the same characters that have here been used to clarify this situation, which demonstrates that it is often not the characters themselves but their interpretation that introduces instability into classifications. Our approach has successfully clarified possible relationships in most groups, although certain problems remain. In particular the newly segregated genus *Aderkomyces*, while having a very stable core group centred around *A. couepiae*, remains a somewhat provisional assemblage. On the other hand, *Gyalideopsis* and *Echinoplaca*, previously believed to represent very heterogeneous entities, in fact proved to be less problematic as to a revised generic delimitation.

Owing to the large size of the data set, especially with regard to the number of taxa, it was necessary to split it into a number of taxa sub-sets to facilitate analysis and study the effects of addition or exclusion of taxa or characters. Indeed, the inclusion of particular taxa or characters changed tree topography in ways that could readily be explained. This indicates that phylogenetic reconstructions based on phenotype data, even if assumed to be 'complete' in terms of the taxa included, do not reproduce the true phylogeny with regard to individual elements, but merely serve as a base for phylogenetic hypotheses. Thus, strict monophyly obtained from a single cladogram cannot be taken as the only criterion to define taxa, and paraphyletic assemblages have to be considered as well.

The partly different phylogenies obtained from comparison of different character sets, such as apothecia *versus* hyphophores, indicates a low degree of correlation in these cases and suggests neither of them necessarily reflects the true phylogeny of the taxa included. The same problem is known from the inclusion of different genotype data sets or the combination of phenotype and genotype data. While this conflict is usually solved by constructing combined data sets or consensus trees, doubt always remains concerning the placement of individual taxa, and this margin of uncertainty is too large for the strict application of cladistic principles in phenotype-based phylogenetic analyses.

Our analysis was especially helpful with regard to the systematic evaluation of certain characters. Thus, black sterile setae and immersed-erumpent, zeorine or carbonized apothecia turned out to represent useful synapomorphies that define large, apparently natural entities. On the other hand, white sterile setae and apothecia with lobulate margins clearly represent homoplasies, and their presence does not necessarily denote close phylogenetic relationship. The seemingly confusing diversity of hyphophore types displays a rather clear structure in the phylogenetic analysis, since most clades are characterized by rather uniform hyphophores, both in terms of morphology and anatomy.

Altogether, our phylogenetic analysis clearly improved our ideas of systematic relationships within the family and the delimitation of taxa at different levels. The trees do not show strong support for all systematic changes proposed here, but we think it is necessary to formally recognize our results, in order to facilitate access to this fascinating family and to formulate clear hypotheses that can be tested by advanced methods such as molecular systematics.

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## Appendix 1. List of taxa used in the phylogenetic analysis

**Outgroup taxon**
*Gyalidea hyalinescens* Vězda

**Ingroup taxa**
*Actinoplaca strigulacea* Müll. Arg.

*Aderkomyces couepiae* Bat.

*Arthotheliopsis hymenocarpoides* Vain.

*Aulaxina aggregata* Lücking & Kalb
*A. corticola* Kalb & Vězda
*A. dictyospora* R. Sant.
*A. epiphylla* (Zahlbr.) R. Sant.
*A. intermedia* Lücking
*A. microphana* (Vain.) R. Sant.
*A. minuta* R. Sant.
*A. multiseptata* R. Sant.
*A. opegraphina* Fée
*A. quadrangula* (Stirt.) R. Sant.
*A. submuralis* Kalb & Vězda
*A. uniseptata* R. Sant.
*A. unispora* Sérus.

*Bullatina aspidota* (Vain.) Vězda & Poelt
*B. microcarpa* Vězda
*B. viridis* Brusse

*Calenia africana* Sérus.
*C. aggregata* R. Sant.
*C. applanata* ad int.
*C. areolata* Lücking
*C. bullatinoides* Lücking
*C. conspersa* (Stirt.) R. Sant.
*C. depressa* Müll. Arg.
*C. dictyospora* Lücking
*C. echinoplacoides* Lücking**
*C. flava* Lücking *et al.*
*C. fumosa* Lücking**
*C. graphidea* Vain.
*C. inconspicua* (Müll. Arg.) R. Sant. & Lücking
*C. leptocarpa* Vain.
*C. lobulata* Lücking
*C. lueckingii* C. Hartmann
*C. maculans* (Vain.) R. Sant.
*C. minuta* Lücking
*C. monospora* Vězda
*C. obtecta* Lücking**
*C. philippinensis* Lücking & Kalb
*C. phyllogena* (Müll. Arg.) R. Sant.
*C. pruinosa* ad int.
*C. rionigrensis* ad int.
*C. rolandiana* C. Hartmann
*C. solorinoides* Lücking
*C. subdepressa* Lücking
*C. submuralis* Lücking
*C. thelotremella* Vain.
*C. triseptata* Zahlbr.

*Caleniopsis laevigata* (Müll. Arg.) Vězda & Poelt
*C. tetramera* Lücking

*Diploschistella urceolata* Vain.

*Echinoplaca amapensis* Bat. & Poroca
*E. atromuralis* Lücking**
*E. atrofusca* R. Sant.
*E. bispora* Kalb & Vězda
*E. campanulata* Kalb & Vězda
*E. diffluens* (Müll. Arg.) R. Sant.
*E. epiphylloides* Lücking**
*E. epiphylla* Fée
*E. furcata* Sérus. var. *furcata*
*E. furcata* subspecies *neotropica* Lücking
*E. fusconitida* Lücking
*E. gemmifera* Lücking
*E. handelii* (Zahlbr.) Lücking
*E. hispida* Sipman
*E. incrustatociliata* Sérus.
*E. intercedens* Vězda

*E. leucotrichoides* (Vain.) R. Sant.
*E. leucomuralis* Lücking**
*E. lucernifera* Kalb & Vězda
*E. macgregorii* (Vain.) Lücking*
*E. madagascariensis* ad. int.
*E. marginata* Lücking
*E. melanotrix* Lücking
*E. pachyparaphysata* R. Sant.
*E. pellicula* (Müll. Arg.) R. Sant.
*E. serusiauxii* Lücking
*E. similis* Kalb & Vězda
*E. streimannii* Sérus.
*E. subsimilis* Kalb & Vězda
*E. tetrapla* (Zahlbr.) Lücking
*E. tricharioides* Kalb & Vězda
*E. triseptata* Lücking
*E. verrucifera* Lücking
*E. vezdana* Lücking & Kalb
*E. wilsonii* Lücking**

*Epilithia cristata* Nyl.

*Gomphillus americanus* Essl.
*G. calycioides* (Del. ex Duby) Nyl.
*G. ophiosporus* Kalb & Vězda

*Gyalectidium areolatum* L. I. Ferraro & Lücking
*G. atrosquamulatum* Lücking & Kalb
*G. australe* Lücking
*G. catenulatum* (Cavalc. & A. A. Silva) L. I. Ferraro *et al.*
*G. caucasicum* (Elenk. & Woron.) Vězda
*G. ciliatum* Thor *et al.*
*G. colchicum* Vězda
*G. conchiferum* Lücking & Wirth
*G. corticola* Henssen
*G. denticulatum* Lücking
*G. eskuchei* Sérus.
*G. fantasticum* L. I. Ferraro & Lücking
*G. filicinum* Müll. Arg.
*G. flabellatum* Sérus.
*G. fuscum* Sérus.
*G. gahavisukanum* Sérus.
*G. imperfectum* Vězda
*G. kenyanum* Lücking & Kalb
*G. laciniatum* Lücking
*G. membranaceum* Sérus.
*G. minor* Sérus.
*G. neotropicum* Lücking
*G. novoguineense* Sérus.
*G. palmicola* Farkas & Vězda
*G. puntilloi* Sérus.
*G. radiatum* Thor *et al.*
*G. setiferum* Vězda & Sérus.
*G. verruculosum* Sérus.
*G. yahriae* Buck & Sérus.

*Gyalideopsis actinoplacoides* Lücking
*G. aequatoriana* Kalb & Vězda
*G. africana* Kalb & Vězda
*G. albopruinosa* Lücking
*G. alnicola* Vězda
*G. anastomosans* P. James & Vězda
*G. argentea* (Mont.) Kalb & Vězda
*G. aterrima* Vězda & Poelt
*G. athalloides* (Nyl.) Vězda
*G. bispora* Vězda
*G. 'brevipilosa'*
*G. 'buckei'*
*G. calabrica* Puntillo & Vězda
*G. capitata* Sérus.
*G. choshuencensis* Lücking & Wirth
*G. cochlearifera* Lücking & Sérus.
*G. confluens* Kalb & Vězda
*G. cyanophila* Sérus.
*G. epithallina* Lücking
*G. formosana* Harada & Vězda
*G. gigantea* Kalb & Vězda
*G. giganteoides* Sérus.
*G. graminicola* Vězda & Kantvilas
*G. haliotidiformis* Kalb & Vězda
*G. hyalina* Lücking
*G. intermedia* Lücking
*G. japonica* Harada & Vězda
*G. kalbii* Vězda
*G. krogiae* Kalb & Vězda
*G. laevithallina* Lücking**
*G. lambinonii* Vězda
*G. lecideina* Kalb & Vězda
*G. lithophila* Thor & Vězda
*G. lobulata* Lücking**
*G. megalospora* Vězda & Poelt
*G. mexicana* Tretiach *et al.*
*G. minima* Vězda
*G. minutissima* Lücking
*G. modesta* Vězda & Poelt
*G. monospora* Kalb & Vězda
*G. montana* Lücking
*G. muscicola* P. James & Vězda
*G. napoensis* Kalb & Vězda
*G. nepalensis* Vězda & Poelt
*G. ochroleuca* Vězda
*G. pallida* Lücking
*G. palmata* Kalb & Vězda
*G. pallescens* Lücking**
*G. parvula* Kalb & Vězda
*G. perlucida* Vězda & Hafellner
*G. perminuta* Vězda
*G. peruviana* Vězda
*G. philippiae* Vězda
*G. poeltii* Vězda
*G. puertoricensis* Lücking & Sipman*
*G. robusta* Kalb & Vězda
*G. rogersii* Vězda & Hafellner
*G. rostrata* Kalb & Vězda
*G. rubescens* Vězda
*G. rubrofusca* Kalb & Vězda
*G. rubra* Lücking
*G. scotica* P. James
*G. solorinellaeformis* Vězda
*G. stipitata* Kalb & Vězda
*G. subantarctica* Henssen & Lumbsch
*G. trapperi* Kalb & Vězda
*G. vainioi* Kalb & Vězda
*G. verruculosa* Vězda & Hafellner

*G. vezdae* Kalb
*G. vivantii* Sérus.
*G. vulgaris* (Müll. Arg.) Lücking
*G. williamsii* Kalb & Vězda
*G. wirthii* Kalb & Vězda
*G. zeylandica* Vězda & Malcolm

*Hippocrepidea nigra* Sérus.

*Microlychnus epicorticis* Funk

*Microspatha glauca* P. Karst.

*Paratricharia paradoxa* (Lücking) Lücking

*Sporocybomyces pulcher* H. Maia

*Tricharia albostrigosa* R. Sant.
*T. albostrigosa* f. *aggregata* Lücking & Vězda**
*T. amazonum* Vain.
*T. armata* Vězda
*T. atrocarpa* Lücking & Sipman*
*T. aulaxiniformis* Lücking & Kalb
*T. aulaxinoides* Kalb & Vězda
*T. carneoalba* Lücking & Kalb
*T. carnea* (Müll. Arg.) R. Sant.
*T. cretacea* Vězda
*T. cubana* Vězda
*T. cuneata* L. I. Ferraro & Vězda
*T. demoulinii* Sérus.
*T. deslooveri* Sérus.
*T. dilatata* Vězda
*T. elegans* Sérus.
*T. farinosa* R. Sant.
*T. fumosa* Kalb & Vězda
*T. guatemalensis* Lücking & Barillas
*T. helminthospora* R. Sant.
*T. heterella* (Stirt.) Lücking
*T. hyalina* Kalb & Vězda
*T. kashiwadanii* Thor *et al.*
*T. lancicarpa* Kalb & Vězda
*T. lobulimarginata* Lücking & Sipman*
*T. longispora* Kalb & Vězda
*T. microtricha* Lücking & Kalb
*T. novoguineensis* Sérus.
*T. pallida* Vězda
*T. papillifera* Lücking
*T. paraguayensis* (L. I. Ferraro & Lücking) Lücking
*T. plana* Vězda
*T. planicarpa* Lücking
*T. pseudosantessonii* Lücking
*T. purulhensis* Lücking & Barillas
*T. ramifera* Sérus.
*T. santessoniana* Kalb & Vězda
*T. santessonii* D. L. Hawksw.
*T. similis* Vězda
*T. subalbostrigosa* Lücking
*T. 'subhelminthospora'**
*T. subplana* Kalb & Vězda
*T. substipitata* Vězda
*T. testacea* Kalb & Vězda
*T. triseptata* R. Sant.
*T. umbrosa* Kalb & Vězda
*T. urceolata* (Müll. Arg.) R. Sant.
*T. vainioi* R. Sant.
*T. variratae* Lücking & Sipman*
*T. verrucifera* Lücking
*T. verrucosa* Sérus.

*new taxon or combination made in this paper (see Appendix 3).
**refers to forthcoming *Flora Neotropica Monograph* of the first author (R. Lücking unpublished).

## Appendix 2. Characters and character state definitions used in the phyogenetic analysis. All characters are binarily coded (abs=absent, pre=present)

**(1) Ecology (14)**

*Lichenization*

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

*Substratum*—Includes taxa attacked by lichenicolous species.

2 Inorganic: 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 (45)**

*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 colour*—A blend of colours 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

*Sterile setae*—We distinguished between taxa in which setae are always present (e.g. *Tricharia* s. str., 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 colour*

46 Red-brown: 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 is 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 colour*

55 Red-brown: 0=abs/1=pre
56 Black colour: 0=abs/1=pre

*Sterile setae second type structure and shape*

57 Shorter than 0·5 mm: 0=abs/1=pre
58 Longer than 1·0 mm: 0=abs/1=pre

*Soralia occurrence*

59 Soralia: 0=abs/1=pre

**(3) Apothecial morphology and anatomy (83)**

*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 colour*

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 colouration: 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
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 Colour 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 (0/0/0/0/0/0).

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

*Ascospore septation*—The default is 1-septate ascospores (0/0/0/0/0/0).

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

*Ascospore shape and size*—The default is 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

**(4) Hyphophores (67)**

*Hyphophore 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
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 Capitate: 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 Mussel-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
165 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 is vertical scales with entire margin and white colour

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 colour*—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 held together or lacking a gelatinous matrix (checked under the microscope under low power). 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 is 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): 0=abs/1=pre
194 Constrictions (throughout): 0=abs/1=pre
195 Bacillar segments: 0=abs/1=pre
196 Thickened hyphae: 0=abs/1=pre
197 Basal branching only: 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

## Appendix 3. New taxa and new combinations in *Gomphillaceae*

### Actinoplaca gemmifera (Lücking) Lücking, Sérus. & Vězda comb. nov.

*Echinoplaca gemmifera* Lücking, *Biblioth. Lichenol.* **65:** 53 (1997).

### Aderkomyces albostrigosus (R. Sant.) Lücking, Sérus. & Vězda comb. nov.

*Tricharia albostrigosa* R. Sant., *Symb. Bot. Ups.* **12**(1): 388 (1952).

### Aderkomyces armatus (Vězda) Lücking, Sérus. & Vězda comb. nov.

*Tricharia armata* Vězda, *Folia Geobot. Phytotax., Praha,* **10:** 404 (1975).

### Aderkomyces brevipilosus (Kalb & Vězda) Lücking, Sérus. & Vězda comb. nov.

*Tricharia brevipilosa* Kalb & Vězda, *Biblioth. Lichenol.* **29:** 61 (1988).

### Aderkomyces carneoalbus (Lücking & Kalb) Lücking, Sérus. & Vězda comb. nov.

*Tricharia carneoalba* Lücking & Kalb, *Bot. Jahrb. Syst.* **122:** 51 (2000).

### Aderkomyces cretaceus (Vězda) Lücking, Sérus. & Vězda comb. nov.

*Tricharia cretacea* Vězda, *Folia Geobot. Phytotax., Praha,* **14:** 72 (1979).

### Aderkomyces cubanus (Vězda) Lücking, Sérus. & Vězda comb. nov.

*Tricharia cubana* Vězda, *Folia Geobot. Phytotax., Praha,* **19:** 198 (1984).

### Aderkomyces deslooveri (Sérus.) Lücking, Sérus. & Vězda comb. nov.

*Tricharia deslooveri* Sérus. in Aptroot *et al., Biblioth. Lichenol.* **64:** 200 (1997).

### Aderkomyces dilatatus (Vězda) Lücking, Sérus. & Vězda comb. nov.

*Tricharia dilatata* Vězda, *Acta Mus. Silesiae, Opava, ser. A,* **22:** 87 (1973).

### Aderkomyces fumosus (Kalb & Vězda) Lücking, Sérus. & Vězda comb. nov.

*Tricharia fumosa* Kalb & Vězda, *Biblioth. Lichenol.* **29:** 64 (1988).

### Aderkomyces guatemalensis (Barillas & Lücking) Lücking, Sérus. & Vězda comb. nov.

*Tricharia guatemalensis* Lücking & Barillas, *Biblioth. Lichenol.* **65:** 81 (1997).

**Aderkomyces heterellus (Stirt.) Lücking, Sérus. & Vězda comb. nov.**

*Arthonia heterella* Stirt., *Proc. Philos. Soc. Glasgow* **11:** 106 (1878); *Echinoplaca heterella* (Stirt.) R. Sant., *Symb. Bot. Ups.* **12**(1): 372 (1952); *Tricharia heterella* (Stirt.) Lücking, *Biblioth. Lichenol.* **65:** 82 (1997).

*Lopadium membranula* Müll. Arg., *J. Linn. Soc. Bot.* **29:** 326 (1892); *Tricharia membranula* (Müll. Arg.) Lücking in Lücking & Lücking, *Herzogia* **11:** 158 (1995).

*Echinoplaca affinis* Kalb & Vězda, *Biblioth. Lichenol.* **29:** 20 (1988).

**Aderkomyces lobulimarginatus Sipman & Lücking sp. nov.**

A *Aderkomycete guatemalense* marginibus apotheciorum lobulis instructis differt.

Typus: Malaysia (Borneo), Sabah, Mt. Kinabalu National Park, 6°05′N, 116°35′E, 1700 m, foliicolous, May 1989, *Sipman & Tan* 29497 (B—holotypus).

*Thallus* foliicolous, crustose, dispersed into small, irregular, slightly inflated patches containing algae and encrusted with crystals, connected by a translucent, thin prothallus, 5–10 mm across; sterile setae numerous, white, rather soft, 0·6–0·8 mm long and basally 30 µm thick.

*Apothecia* numerous, rounded, 0·25–0·5 mm diam., at first covered by thin thallus tissue which ruptures into usually four triangular lobes, greyish black, later the lobes disappearing and exposing the dark brown disc and finally the blackish brown margin; mature apothecia finally sessile with distinct, slightly prominent proper margin and without lobes, dark brown to blackish brown; *exciple* well developed, composed of rather dense branched hyphae and therefore almost prosoplectenchymatous, walls dark brown, especially in upper part, 30–40 µm laterally; *hypothecium* thin, 5–10 µm, brown; *hymenium* colourless, 90–110 µm; *asci* 80–90 × 30–40 µm; *ascospores* (1–)2 per ascus, richly muriform, broadly ellipsoid, 40–70 × 25–40 µm. *Hyphophores* abundant, setiform, pale but apically slightly darkened, not broadened, diahyphae inserted below the apex, 0·4–0·5 mm high and 25 µm broad at base; diahyphae filiform but apically moniliform, segmented, final segments elongate ellipsoid to broadly bacilar, 15 × 3 µm, 3-septate, with rounded apex, subapical segments non-septate, rounded or elongate, connected by thin intercalar threads.

*Notes.* This new species resembles *Aderkomyces guatemalensis* but differs in a number of features, such as the darker, lobulate apothecia, the larger ascospores, and the slightly different hyphophores.

**Aderkomyces microcarpus (Etayo & Lücking) Lücking, Sérus. & Vězda comb. nov.**

*Tricharia microcarpa* Etayo & Lücking in Etayo, Aportación al catálogo de líquenes epífilos y hongos liquenícolas de Coiba (Panamá). (1997).

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

*Tricharia microtricha* Lücking & Kalb, *Bot. Jahrb. Syst.* **122:** 51 (2000).

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

*Tricharia papillifera* Lücking, *Biblioth. Lichenol.* **65:** 85 (1997).

**Aderkomyces planus (Vězda) Lücking, Sérus. & Vězda comb. nov.**

*Tricharia plana* Vězda, *Folia Geobot. Phytotax., Praha,* **14:** 74 (1979).

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

*Tricharia purulhensis* Barillas & Lücking, *Biblioth. Lichenol.* **65:** 88 (1997).

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

*Tricharia ramifera* Sérus. in Aptroot *et al.*, *Biblioth. Lichenol.* **64:** 202 (1997)

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

*Tricharia subalbostrigosa* Lücking, *Biblioth. Lichenol.* **65:** 89 (1997).

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

*Tricharia subplana* Kalb & Vězda, *Biblioth. Lichenol.* **29:** 71 (1988)

**Aderkomyces testaceus (Kalb & Vězda) Lücking, Sérus. & Vězda comb. nov.**

*Tricharia testacea* Kalb & Vězda, *Biblioth. Lichenol.* **29:** 73 (1988)

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

*Tricharia verrucifera* Lücking, *Willdenowia* **29:** 319 (1999).

**Aderkomyces verrucosus (Sérus.) Lücking, Sérus. & Vězda comb. nov.**

*Tricharia verrucosa* Sérus. in Aptroot *et al.*, *Biblioth. Lichenol.* **64:** 204 (1997).

**Aplanocalenia Lücking, Sérus. & Vězda gen. nov.**

A *Calenia* apotheciis planis in thallo immersa margine nulla differt.

Typus: *Aplanocalenia inconspicua* (Müll. Arg.) Lücking, Sérus. & Vězda [≡*Heterothecium inconspicuum* Müll. Arg.] (holotypus).

*Notes*. Differing from *Calenia* s. str. by the completely immersed, translucent apothecia lacking a prominent margin. Apart from the type species, which is represented by very depauperate type material, there are perhaps two further taxa waiting formal recognition. They are identical to *Aplanocalenia inconspicua* but differ slightly in their ascospore septation (Santesson & Lücking 1999).

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

*Heterothecium inconspicuum* Müll. Arg., *Lichenes Epiphylli Novi*: 14 (1890).

**Arthotheliopsis planicarpa (Lücking) Lücking, Sérus. & Vězda comb. nov.**

*Tricharia planicarpa* Lücking, *Biblioth. Lichenol.* **65:** 86 (1997).

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

*Echinoplaca serusiauxii* Lücking, *Biblioth. Lichenol.* **65:** 60 (1997).

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

*Echinoplaca tricharioides* Kalb & Vězda, *Biblioth. Lichenol.* **29:** 28 (1988).

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

*Calenia aggregata* R. Sant., *Symb. Bot. Ups.* **12**(1): 343 (1952).

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

*Thelotrema conspersa* Stirt., *Proc. Philos. Soc. Glasgow* **11:** 101 (1878); *Calenia conspersa* (Stirt.) R. Sant., *Symb. Bot. Ups.* **12**(1): 340 (1952).

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

*Gyalideopsis lithophila* Thor & Vězda, *Folia Geobot. Phytotax., Praha* **19:** 77 (1984).

**Diploschistella solorinellaeformis (Vězda) Lücking, Sérus. & Vězda comb. nov.**

*Gyalideopsis solorinellaeformis* Vězda, *Folia Geobot. Phytotax., Praha* **14:** 68 (1979).

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

*Gyalideopsis trapperi* Kalb & Vězda, *Biblioth. Lichenol.* **29:** 49 (1988).

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

*Arthonia macgregorii* Vain., *Ann. Acad. Sci. Fenn., Ser. A,* **15:** 313 (1921).

**Ferraroa Lücking, Sérus. & Vězda gen. nov.**

A *Gyalideopsis* hyphophoris campilidiis similibus differt.
Typus: *Ferraroa hyalina* (Lücking) Lücking, Sérus. & Vězda [≡*Gyalideopsis hyalina* Lücking] (holotypus).

*Notes.* Differing from *Gyalideopsis* s. str. by the camplidioid hyphophores. This new genus is dedicated to our friend and colleague, Dr Lidia Ferraro, for her many contributions to lichenology in southern South America, and to our knowledge of *Gomphillaceae*.

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

*Gyalideopsis hyalina* Lücking, *Biblioth. Lichenol.* **65:** 67 (1997).

**Gyalideopsis buckei Lücking, Sérus. & Vězda nom. nov.**

*Tricharia vezdae* W. R. Buck, *Brittonia* **32:** 222 (1980); non *Gyalideopsis vezdae* Kalb, *Schedae ad Lichenes Neotropici* **4:** no. 229 (1983).

**Gyalideopsis brevipilosa (Kalb & Vězda) Lücking, Sérus. & Vězda comb. nov.**

*Tricharia brevipilosa* Kalb & Vězda, *Biblioth. Lichenol.* **29:** 61 (1988).

**Gyalideopsis cristata (Vain.) Lücking, Sérus. & Vězda comb. nov.**

*Epilithia cristata* Nyl., *Collect. Lichenol.* **16:** (1853).

**Gyalideopsis glauca (P. Karst.) Lücking, Sérus. & Vězda comb. nov.**

*Microspatha glauca* P. Karst., *Revue Mycol.* **11:** 207 (1889).

**Gyalideopsis puertoricensis Sipman & Lücking sp. nov.**

A *Gyalideopsis palmata* hyphophoribus longioribus pallidioribusque et exciplo prosoplectenchymatico differt.
Typus: Puerto Rico, Ponce, Caribbean National Forest, Toro Negro Division, 18°09′N, 66°34′W, 1150 m, corticolous, May 1989, *Sipman* 25846 (B—holotypus).

*Thallus* corticolous, smooth but irregularly cracked here and there, pale whitish grey, slightly nitidous, *c.* 50 µm thick, with cartilaginous, corticiform layer.

*Apothecia* numerous, rounded, 0·25–0·40 mm diam., plane but with distinct, prominent margin and basally slightly constricted; in dry condition dark reddish brown to almost black, in moist condition disc reddish brown and margin blackish; *excipulum* well developed, laterally up to 50 µm thick, composed of branched hyphae but very dense and partly appearing prosoplectenchymatous, yellowish brown, inner parts of lateral exciple bordering the hymenium dark brown; *epithecium* thin but distinctly pigmented, 5 µm, yellowish brown; *hypothecium* prosoplectenchymatous, 10–15 µm, colourless to very pale yellowish in central parts; *hymenium* colourless, 65–75 µm high; *paraphyses* richly branched and anastomosing; *ascospores* single, richly muriform, 30–50 × 20–25 µm, mostly young, only few found mature. *Hyphophores* scattered, difficult to distinguish on parts of thalli growing between small bryophytes or algae, pale (bluish) grey to pale brown, setiform but with upper part strongly expanded, 0·25–0·30 mm high, stipe 50 µm thick, upper part 0·15–0·17 mm broad, in shape of a semicircle, margin irregularly incised and whole plate with cellular structure, leptodermatous; *diahyphae* multiseptate, up to 50 µm long and 1·5–2·5 µm broad, filiform with slight constrictions, apical part (25 µm) composed of rather short, barrel-shaped cells (2–3 × 1·5–2 µm), basal part cells longer (6–8 × 2–2.5 µm).

*Notes.* This new species belongs in the *Gyalideopsis palmata* group, because of its flabelliform hyphophores producing moniliform diahyphae. Within that section, three other species have single-spored asci with muriform ascospores. *Gyalideopsis gigantea* clearly differs by its very large hyphophores with tomentose stipe, while *G. palmata* and *G. vainioi* have black hyphophores with very short stipes. In addition, *G. puertoricensis* can be distinguished from these and other species of this group by its almost prosoplectenchymatous excipulum.

*Additional specimens examined.* **Guadeloupe**: Basse-Terre, Mamelle du Petit Bourg, 700 m, 1996, *Sérusiaux* 17169 (LG); *ibid.*, NE de La Madeleine, chemin allant du Grand Etang vers l'Etang de l'As de Pique, 400–450, 1996, *Sérusiaux* 17169 (LG).

## Jamesiella Lücking, Sérus. & Vězda gen. nov.

A *Gyalideopsis* hyphophoribus isidiiformibus differt.

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

*Notes.* Differing from *Gyalideopsis* s. str. by the isidiiform hyphophores ('thlasidia'), which are interpreted as transformed stipitate hyphophores in which the diahyphae are produced internally instead of externally, and the whole hyphophore is dispersed as an entity and functions as a diaspore. Dedicated to Peter James for his outstanding contributions to lichenology.

## Jamesiella anastomosans (P. James & Vězda) Lücking, Sérus. & Vězda comb. nov.

*Gyalideopsis anastomosans* P. James & Vězda in Vězda, *Folia Geobot. Phytotax., Praha* 7: (1972).

## Jamesiella perlucida (Vězda & Hafellner) Lücking, Sérus. & Vězda comb. nov.

*Gyalideopsis perlucida* Vězda & Hafellner, *Preslia* 60: 239 (1988).

## Jamesiella scotica (P. James) Lücking, Sérus. & Vězda comb. nov.

*Gyalideopsis scotica* P. James, *Lichenologist* 7: (1975).

## Lithogyalideopsis Lücking, Sérus. & Vězda gen. nov.

A *Gyalideopsis* hyphophoribus typi *Aulaxinae* differt.

Typus: *Lithogyalideopsis poeltii* (Vězda) Lücking, Sérus. & Vězda [≡ *Gyalideopsis poeltii* Vězda] (holotypus).

*Notes.* Differing from *Gyalideopsis* s. str. by the *Aulaxina*-type hyphophores, which are setiform, black, and produce 'palmate' diahyphal bunches, i.e. the diahyphae consist of 3–5 individual, much branched bunches that are connected to the apex of the stipe by means of rather thick, unbranched hyphal cords formed by agglutinate hyphae.

## Lithogyalideopsis aterrima (Vězda & Poelt) Lücking, Sérus. & Vězda comb. nov.

*Gyalideopsis aterrima* Vězda & Poelt, *Herzogia* 2: (1973).

## Lithogyalideopsis poeltii (Vězda) Lücking, Sérus. & Vězda comb. nov.

*Gyalideopsis poeltii* Vězda, *Mitt. Bot. Staatsamml. München* 19: 155 (1983).

## Lithogyalideopsis vivantii (Sérus.) Lücking, Sérus. & Vězda comb. nov.

*Gyalideopsis vivantii* Sérus., *Nova Hedwigia* 67: 393 (1998).

## Lithogyalideopsis zeylandica (Vězda & Malcolm) Lücking, Sérus. & Vězda comb. nov.

*Gyalideopsis zeylandica* Vězda & Malcolm, *Australasian Lichenol. Newsl.* 40: 20 (1997).

## Rubrotricha Lücking, Sérus. & Vězda gen. nov.

A *Tricharia* setis rubrofuscis et hyphophoribus pallidis et excipulo apotheciorum e hyphis ramosis differt.

Typus: *Rubrotricha helminthospora* (R. Sant.) Lücking, Sérus. & Vězda [≡ *Tricharia helminthospora* R. Sant.] (holotypus).

*Notes*. Differing from *Tricharia* s. str. by the dark reddish brown setae with pale tips, the pale to reddish brown hyphophores and the hyphal excipulum being composed of branched and anastomosing hyphae.

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

*Tricharia helminthospora* R. Sant., *Symb. Bot. Ups.* 12(1): 381 (1952).

**Rubrotricha subhelminthospora Lücking sp. nov.**

A *Rubrotricha helminthospora* hyphophoribus setiformis apice acutis et setis angustioribus differt.

Typus: Ecuador, Napo, Jatun Satcha Biological Station, 25 km E of Tena, 450 m, v 1996, *Lücking* 96908 (QCNE—holotypus).

*Notes:* Differing from *Rubrotricha helminthospora* in the long-setiform hyphophores with acute apex and narrower thallus setae. Because of its identical apothecial morphology and ascospore type, this neotropical taxon (Lücking 2005) had previously been identified with the paleotropical *Tricharia* (≡*Rubrotricha*) *helminthospora*. However, the discovery of setiform hyphophores with acute apices demonstrates that it represents a different species. The two taxa can thus be separated in the same way as the neotropical *Aderkomyces papilliferus* and the African paleotropical *A. dilatatus* (Lücking 1997).

**Tricharia atrocarpa Lücking & Sipman sp. nov.**

*Tricharia* apotheciis nigris et ascosporis 3-septatis.

Typus: Malaysia (Borneo), Sabah, Mt. Kinabalu National Park, 6°05′N, 116°35′E, 1800 m, foliicolous, May 1989, *Sipman* 30899 (B—holotypus).

*Thallus* foliicolous, crustose, 5–10 mm diam., pale greenish to whitish grey, with slightly irregular surface. Sterile setae black, 0·5–1 mm long.

*Apothecia* numerous, rounded, 0·2–0·3 mm diam., black even when moist, strongly concave to almost urceolate, with deeply submersed disc and strongly prominent, thin margin; *excipulum* brownish black, without visible structure, 25–30 µm thick; *hypothecium* dark brownish black, 10–15 µm; *hymenium* colourless, 50 µm; *paraphyses* richly branched and anastomosing; *asci* narrowly clavate, 50 × 12; *ascospores* 3-septate, slightly constricted at septa, 10–12 × 3–3.5 µm; hyphophores not observed.

*Notes.* This new species is easily distinguished from all other species of the genus by its genuinely lecideine apothecia and 3-septate ascospores. Most species of *Tricharia* have rather pale, translucent apothecia; a few, such as *T. farinosa* and *T. pseudosantessonii*, feature dark brown apothecia, but differ in their submuriform to muriform ascospores.

**Tricharia variratae Lücking & Sipman sp. nov.**

A *Tricharia pallida* hyphophoribus umbelliformibus differt.

Typus: Papua New Guinea, Central Province, Varirata National Park, 9°27′S, 147°22′E, 800 m, foliicolous, March 1987, *Sipman* 22455c (B—holotypus!).

*Thallus* foliicolous, crustose, 5–20 mm across, greyish green, smooth, continuous, without crystals; setae abundant, black, 0·7–1·0 mm long and basally 40–50 µm thick, tip often pale.

*Apothecia* not abundant, sessile, very strongly constricted basally and with short, thick stipe, regularly rounded, 0·4–0·7 mm diam and 0·3–0·4 mm high, disc plane, pale yellowish brown, translucent, margin thin, not or slightly prominent, somewhat darker; *exciple* composed of branched hyphae embedded in gelatinous matrix, hyaline, well developed, reaching down the stipe to apothecial base; *hypothecium* thin, 10–15 µm, hyaline, prosoplectenchymatous; central apothecial base composed of densely interwoven to prosoplectenchymatous hyphae anticlin, hyaline; *hymenium* hyaline, 75 µm; *paraphyses* branched and anastomosing; asci clavate, 60–65 10–13 µm; *ascospores* 6–8 per ascus, ellipsoid, submuriform, with 3–5 × 0–1 septa, 15–18 × 5–7 µm. *Hyphophores* abundant, setiform, black, 0.8–1.2 mm long and basally 40–

50 µm broad, not distincly tapering apically, uppermost part expanded to form a disc-like, palmate to lobate shield 0.15–0.2 mm diam when moist, lobes formed by a single layer of parallel hyphae, with dark brown walls, hyphae *c.* 2 µm diam. *Diahyphae* not observed.

*Notes.* *Tricharia variratae* seems to be closely related to *T. elegans* and related species. It is very similar to *T. pallida* but can be distinguished from this and other species by its more or less umbelliform (nail-like) hyphophores. The last species have hyphophores and/or thallus setae that feature a crown of apical hooks, rather than a disc-like expansion.

## Appendix 4. Systematic outline of the lichen family *Gomphillaceae* (in systematic order following their arrangement in the phylogenetic analysis)

**1. *Diploschistella* Vain.**
*D. lithophila* (Thor & Vězda) Lücking, Sérus & Vězda
*D. solorinellaeformis* (Vězda) Lücking, Sérus & Vězda
*D. trapperi* (Kalb & Vězda) Lücking, Sérus & Vězda
*D. urceolata* Vain.*

**2. *Lithogyalideopsis* Lücking, Sérus. & Vězda**
*L. aterrima* (Vězda & Poelt) Lücking, Sérus. & Vězda
*L. poeltii* (Vězda) Lücking, Sérus. & Vězda
*L. vivantii* (Sérus.) Lücking, Sérus. & Vězda
*L. zeylandica* (Vězda & Malcolm) Lücking, Sérus. & Vězda

**3. *Gyalideopsis* Vězda**
*G. actinoplacoides* Lücking
*G. aequatoriana* Kalb & Vězda
*G. africana* Kalb & Vězda
*G. albopruinosa* Lücking
*G. alnicola* W. J. Noble & Vězda*
*G. applanata* Herrera-Campos & Lücking
*G. argentea* (Mont.) Kalb & Vězda
*G. arvidssonii* Lücking
*G. bispora* Vězda
*G. buckei* Lücking, Sérus. & Vězda
*G. calabrica* Puntillo & Vězda*
*G. capitata* Sérus.
*G. choshuencensis* Lücking & Wirth
*G. cochlearifera* Lücking & Sérus.
*G. confluens* Kalb & Vězda
*G. cristata* (Vain.) Lücking, Sérus. & Vězda
*G. cyanophila* Sérus.
*G. epithallina* Lücking
*G. floridae* Etayo & Diederich
*G. formosana* Harada & Vězda
*G. gigantea* Kalb & Vězda
*G. giganteoides* Sérus.
*G. glauca* (P. Karst.) Lücking, Sérus. & Vězda
*G. graminicola* Vězda & Kantvilas
*G. haliotidiformis* Kalb & Vězda
*G. helvetica* Van den Boom & Vězda
*G. intermedia* Lücking
*G. japonica* Harada & Vězda
*G. kalbii* Vězda
*G. krogiae* Kalb & Vězda
*G. laevithallina* Lücking
*G. lambinonii* Vězda
*G. lecideina* Kalb & Vězda
*G. lobulata* Lücking
*G. megalospora* Vězda & Poelt
*G. mexicana* Tretiach *et al.*
*G. minima* Vězda
*G. minutissima* Lücking
*G. modesta* Vězda & Poelt
*G. monospora* Kalb & Vězda
*G. montana* Lücking
*G. moodyae* Lendemer & Lücking
*G. muscicola* P. James & Vězda var. *muscicola*
*G. muscicola* var. *alba* Vězda & Tønsberg
*G. napoensis* Kalb & Vězda
*G. nepalensis* Vězda & Poelt
*G. ochroleuca* Vězda
*G. pallescens* Lücking
*G. pallida* Lücking
*G. palmata* Kalb & Vězda
*G. parvula* Hafellner & Vězda
*G. perminuta* Vězda
*G. peruviana* Vězda
*G. philippiae* Vězda
*G. piceicola* (Nyl.) Vězda & Poelt*
*G. puertoricensis* Lücking & Sipman
*G. robusta* Kalb & Vězda
*G. rogersii* Vězda & Hafellner
*G. rostrata* Kalb & Vězda
*G. rubescens* Vězda
*G. rubra* Lücking
*G. rubrofusca* Kalb & Vězda
*G. stipitata* Kalb & Vězda
*G. subantarctica* Henssen & Lumbsch
*G. tuerkii* Vězda
*G. vainioi* Kalb & Vězda
*G. verruculosa* Vězda & Hafellner
*G. vezdae* Kalb
*G. vulgaris* (Müll. Arg.) Lücking f. *vulgaris*
*G. vulgaris* f. *albopruinosa* Lücking
*G. williamsii* Kalb & Vězda
*G. wirthii* Kalb & Vězda

**4. *Jamesiella* Lücking, Sérus. & Vězda**
*J. anastomosans* (P. James & Vězda) Lücking, Sérus. & Vězda
*J. perlucida* (Vězda & Hafellner) Lücking, Sérus. & Vězda
*J. scotica* (P. James) Lücking, Sérus. & Vězda

**5. *Gomphillus* Nyl.**

*G. americanus* Essl.
*G. calycioides* (Delise ex Duby) Nyl.
*G. caribaeus* W. R. Buck
*G. ophiosporus* Kalb & Vězda

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

**7. *Hippocrepidea* Sérus.**
*H. nigra* Sérus.

**8. *Tricharia* Fée**
*T. amazonum* Vain.
*T. atrocarpa* Lücking & Sipman ined.
*T. aulaxiniformis* Lücking & Kalb
*T. aulaxinoides* Kalb & Vězda
*T. carnea* (Müll. Arg.) R. Sant.
*T. cuneata* L. I. Ferraro & Vězda
*T. demoulinii* Sérus.
*T. elegans* Sérus.
*T. farinosa* R. Sant.
*T. hyalina* Vězda
*T. kashiwadanii* Thor, Lücking & Matsumoto
*T. lancicarpa* Kalb & Vězda
*T. longispora* Kalb & Vězda
*T. novoguineensis* Sérus.
*T. oaxacae* Herrera-Campos & Lücking
*T. pallida* Vězda
*T. paraguyaensis* (L. I. Ferraro & Lücking) Lücking
*T. pseudosantessonii* Lücking
*T. santessoniana* Kalb & Vězda
*T. santessonii* D. Hawksw.
*T. similis* Vězda
*T. sublancicarpa* Herrera-Campos & Lücking
*T. substipitata* Vězda
*T. triseptata* R. Sant.
*T. umbrosa* Kalb & Vězda
*T. urceolata* (Müll. Arg.) R. Sant.
*T. vainioi* R. Sant.
*T. variratae* Lücking & Sipman

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

**10. *Aderkomyces* Bat.**
*A. albostrigosus* (R. Sant.) Lücking, Sérus. & Vězda
*A. albostrigosus* f. *aggregatus* Lücking & Vězda
*A. armatus* (Vězda) Lücking, Sérus. & Vězda
*A. brevipilosus* (Kalb & Vězda) Lücking, Sérus. & Vězda
*A. carneoalbus* (Lücking & Kalb) Lücking, Sérus. & Vězda
*A. couepiae* Bat.
*A. cretaceus* (Vězda) Lücking, Sérus. & Vězda
*A. cubanus* (Vězda) Lücking, Sérus. & Vězda
*A. deslooveri* (Sérus.) Lücking, Sérus. & Vězda
*A. dilatatus* (Vězda) Lücking, Sérus. & Vězda
*A. fumosus* (Kalb & Vězda) Lücking, Sérus. & Vězda
*A. guatemalensis* (Barillas & Lücking) Lücking, Sérus. & Vězda
*A. heterellus* (Stirt.) Lücking, Sérus. & Vězda
*A. lobulimarginatus* Lücking & Sipman
*A. microtrichus* (Lücking & Kalb) Lücking, Sérus. & Vězda
*A. papilliferus* (Lücking) Lücking, Sérus. & Vězda
*A. planicarpus* (Lücking) Lücking, Sérus. & Vězda
*A. planus* (Vězda) Lücking, Sérus. & Vězda
*A. purulhensis* (Barillas & Lücking) Lücking, Sérus. & Vězda
*A. ramiferus* (Sérus.) Lücking, Sérus. & Vězda
*A. subalbostrigosus* (Lücking) Lücking, Sérus. & Vězda
*A. subplanus* (Kalb & Vězda) Lücking, Sérus. & Vězda
*A. testaceus* (Kalb & Vězda) Lücking, Sérus. & Vězda
*A. verruciferus* (Lücking) Lücking, Sérus. & Vězda
*A. verrucosus* (Sérus.) Lücking, Sérus. & Vězda

**11. *Arthotheliopsis* Vain.**
*A. hymenocarpoides* (Vain.) Lücking, Sérus. & Vězda
*A. serusiauxii* (Lücking) Lücking, Sérus. & Vězda
*A. tricharioides* (Kalb & Vězda) Lücking, Sérus. & Vězda

**12. *Echinoplaca* Fée**
*E. amapensis* Bat. & Poroca
*E. atrofusca* R. Sant.
*E. atromuralis* Lücking
*E. bispora* Kalb & Vězda
*E. campanulata* Kalb & Vězda
*E. diffluens* (Müll. Arg.) R. Sant.
*E. epiphylla* Fée
*E. epiphylloides* Lücking
*E. furcata* Sérus. subsp. *furcata*
*E. furcata* subsp. *neotropica* Lücking
*E. fusconitida* Lücking
*E. handelii* (Zahlbr.) Lücking
*E. hispida* Sipman
*E. incrustatociliata* Sérus.
*E. intercedens* Vězda
*E. leucomuralis* Lücking
*E. leucotrichoides* (Vain.) R. Sant.
*E. lucernifera* Kalb & Vězda
*E. macgregorii* (Vain.) Lücking
*E. madagascariensis* ad int.
*E. marginata* Lücking
*E. melanotrix* Lücking
*E. pachyparaphysata* R. Sant.
*E. pellicula* (Müll. Arg.) R. Sant.
*E. similis* Kalb & Vězda
*E. streimannii* Sérus.
*E. subsimilis* Kalb & Vězda
*E. tetrapla* (Zahlbr.) Lücking
*E. triseptata* Lücking
*E. verrucifera* Lücking
*E. vezdana* Lücking & Kalb
*E. wilsonii* Lücking

**13. *Actinoplaca* Müll. Arg.**
*A. gemmifera* (Lücking) Lücking, Sérus. & Vězda
*A. strigulacea* Müll. Arg.

**14. *Calenia* Müll. Arg.**
*C. africana* Sérus.
*C. areolata* Lücking
*C. aspidota* (Vain.) Vězda
*C. aurantiaca* Lücking, Sérus. & Sipman

*C. bullatinoides* Lücking
*C. corticola* (Henssen) L. I. Ferraro, Lücking & Sérus.
*C. depressa* Müll. Arg.
*C. dictyospora* Lücking
*C. echinoplacoides* Lücking
*C. flava* Lücking, Sérus. & Sipman
*C. fumosa* Lücking
*C. graphidea* Vain.
*C. leptocarpa* Vain.
*C. lobulata* Lücking
*C. lueckingii* C. Hartmann
*C. maculans* (Vain.) R. Sant.
*C. minuta* Lücking
*C. monospora* Vězda*
*C. obtecta* Lücking
*C. philippinensis* Lücking & Kalb
*C. phyllogena* (Müll. Arg.) R. Sant.
*C. pruinosa* ad int.
*C. rolandiana* C. Hartmann
*C. solorinoides* Lücking
*C. subdepressa* Lücking
*C. submuralis* Lücking
*C. thelotremella* Vain.
*C. triseptata* Zahlbr.
*C. viridis* (Brusse) Lücking, Sérus. & Vězda

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

**16. *Caleniopsis* Vězda & Poelt**
*C. aggregata* (R. Sant.) Lücking, Sérus. & Poelt
*C. conspersa* (Stirt.) Lücking, Sérus. & Vězda
*C. laevigata* (Vain.) Vězda & Poelt
*C. tetramera* Lücking

**17. *Aulaxina* Fée**
*A. aggregata* Lücking & Kalb
*A. corticola* Kalb & Vězda
*A. dictyospora* R. Sant.
*A. epiphylla* (Zahlbr.) R. Sant.
*A. intermedia* Lücking
*A. microphana* (Vain.) R. Sant.
*A. minuta* R. Sant.
*A. multiseptata* R. Sant.
*A. opegraphina* Fée
*A. quadrangula* (Stirt.) R. Sant.
*A. submuralis* Kalb & Vězda
*A. uniseptata* R. Sant.
*A. unispora* Sérus.

**18. *Paratricharia* Lücking**
*P. paradoxa* (Lücking) Lücking

**19. *Gyalectidium* Müll. Arg.**
**[Sectio *Gyalectidium* Series *Gyalectidium*]**
*G. atrosquamulatum* Lücking & Kalb
*G. aurelii* L. I. Ferraro & Lücking
*G. cinereodiscus* Herrera-Camp. & Lücking
*G. colchicum* Vězda
*G. eskuchei* Sérus.
*G. filicinum* Müll. Arg.
*G. fuscum* Lücking & Sérus.
*G. imperfectum* Vězda
*G. laciniatum* Lücking
*G. pallidum* Herrera-Camp. & Lücking
*G. radiatum* Thor, Lücking & Matsumoto
*G. rosae-emiliae* Herrera-Camp. & Lücking
*G. setiferum* Vězda & Sérus.
*G. verruculosum* Sérus.
**[Sectio *Areolectidium* Series *Areolatae*]**
*G. areolatum* L. I. Ferraro & Lücking
*G. catenulatum* (Cavalc. & Silva) L. I. Ferraro *et al.*
*G. conchiferum* Lücking & Wirth
*G. fantasticum* L. I. Ferraro & Lücking
*G. floridense* Safranek & Lücking
*G. membranaceum* Sérus.
*G. nashii* Herrera-Camp. & Lücking
*G. palmicola* Farkas & Vězda
*G. paolae* Herrera-Camp. & Lücking
*G. plicatum* L. I. Ferraro & Lücking
*G. puntilloi* Sérus.
*G. sanmartinense* Herrera-Camp. & Lücking
**[Sectio *Placolectidium* Series *Caucasicae*]**
*G. australe* Lücking
*G. barbatum* Herrera-Camp. & Lücking
*G. caucasicum* (Elenk. & Woron.) Vězda
*G. chilense* Cáceres & Lücking
*G. ciliatum* Thor, Lücking & Matsumoto
*G. denticulatum* Lücking
*G. flabellatum* Sérus.
*G. gahavisukanum* Sérus.
*G. kenyanum* Lücking & Kalb
*G. maracae* Lücking
*G. minus* Sérus.
*G. novoguineense* Sérus.
*G. ulloae* Herrera-Camp. & Lücking
**[Sectio *Setolectidium* Series *Microcarpae*]**
*G. microcarpum* (Vězda) Lücking, Sérus. & Vězda
**[Sectio** *Goniolectidium* Series *Yahriae*]
*G. yahriae* Buck & Sérus.

**Gyalideopsis athalloides* Vězda is a synonym of *Diploschistella urceolata*; *Gyalideopsis calabrica* is most probably a synonym of *G.muscicola* (diahyphae of the latter were wrongly interpreted in the original descron of the former); *Bullatina viridis* is most probably a synonym of *Calenia monospora* (the latter two to be checked; included here on a provisional basis); *Gyalideopsis alnicola* and *G. piceicola* are here treated separately following Vězda (2003), their proposed synonym status remains to be checked (both supposed to differ in apothecial size).