



A world monograph of the lichen genus *Gyalectidium* (Gomphillaceae)

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Received December 2000; accepted for publication June 2001

Seventeen new species of *Gyalectidium* have been discovered in various parts of the world, and those unexpected findings formed the starting point for a survey of the taxonomy and ecogeography of the genus. The following species are described as new in this paper: *G. areolatum* Ferraro & Lücking (Neotropics), *G. atosquamulatum* Lücking & Kalb (Kenya), *G. australe* Lücking (Australia), *G. conchiferum* Lücking & Wirth (Chile), *G. denticulatum* Lücking (Costa Rica), *G. fantasticum* Ferraro & Lücking (Neotropics), *G. flabellatum* Sérus. (Australasia), *G. fuscum* Lücking & Sérus. (Africa and Papua New Guinea), *G. gahavisukanum* Sérus. (Papua New Guinea), *G. keryanum* Lücking & Kalb (Kenya), *G. laciniatum* Lücking (Costa Rica), *G. maracae* Lücking (Neotropics), *G. membranaceum* Sérus. & Lücking (Canary Islands), *G. minus* Sérus. (Canary Islands and southern Italy), *G. novoguineense* Sérus. (Australasia), *G. puntilloi* Sérus. (south-west Europe), and *G. verruculosum* Sérus. (Australasia). *Calenia microcarpa* Vězda [Syn.: *Bullatina microcarpa* (Vězda) Brusse] is included in *Gyalectidium* as *G. microcarpum* (Vězda) Lücking, Sérus. & Vězda **comb. nov.**, and *G. catenulatum* (Cavalc. & A. A. Silva) Ferraro, Lücking & Sérus. is treated as a species different from *G. filicinum*. *Gyalectidium corticola* Henssen is transferred to *Calenia* as *Calenia corticola* (Henssen) Ferraro, Lücking & Sérus. **comb. nov.** A key to all 29 accepted species of *Gyalectidium* is provided. The infrageneric phylogeny is constructed by means of a phenotype-based cladistic analysis, and the systematic affinities of the genus are discussed, accompanied by notes on the distribution and ecology of the species. Apothecia are not yet known in several species, including new ones.

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ADDITIONAL KEY WORDS: foliicolous lichens – hyphophores – key – phylogeny – taxonomy.

INTRODUCTION

The genus *Gyalectidium* was established by Müller Argoviensis (1881) for a group of three new species of foliicolous lichens with single, muriform ascospores and epithelial algae: *G. dispersum*, *G. filicinum* and *G. xantholeucum*. Müller Argoviensis (1888, 1890, 1891) eventually described two further species, *G. rotuliforme* and *G. argillaceum*, transferred *Biatora phyllocharis* Mont. to *Gyalectidium*, and reduced *G. dispersum* into synonymy with it.

In his outstanding monograph on foliicolous lichens, Santesson (1952) confirmed Zahlbruckner's view of *Gyalectidium* to be heterogeneous, as it included species belonging to at least two different genera in two

different families and orders. In Zahlbruckner's *Catalogus* (1924) and Santesson's monograph (1952), *G. argillaceum*, *G. dispersum*, *G. phyllocharis*, and *G. xantholeucum* are included in the genus *Sporopodium* (Lecanorales: Lecideaceae s.l.; now in the Ectolechiaceae; Vězda, 1986). Indeed, Santesson (1952) adopted a restricted concept of *Gyalectidium*, considering only *G. filicinum* (selected as the type species) and *G. rotuliforme* as belonging to it, and further included *G. aspidotum*, originally described as *Ectolechia aspidota* by Vainio (1901).

Following Santesson (1952), *Gyalectidium* was characterized by a corticate thallus, immersed apothecia with thalline margin and epithelial algae, non-amyloid hymenium, unbranched or branched and anastomosing paraphyses, and 1-spored asci with muriform ascospores. The genus was included in the family Asterothyriaceae (Graphidales) and related to *Calenia*,

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which according to Santesson (1952) differed by a non-corticate thallus, absence of epithelial algae, and transversely septate ascospores.

During the sixties, the group of scientists around the Brazilian mycologist Batista described several anamorphic foliicolous lichen genera with distinctive conidiomata. Some of these, e.g. *Aderkomyces couepiae* (Batista, 1961), eventually turned out to be the highly distinctive structures, described as hyphophores by Vězda (1973, 1979), for some members of the Asterothyriaceae (Lücking *et al.*, 1998). Besides the branched and anastomosing paraphyses, the presence of hyphophores separated the Gomphillaceae (with hyphophores) from the Asterothyriaceae *s.s.* (without hyphophores), and their morphology formed the basis for a new generic concept within the Gomphillaceae (Vězda & Poelt, 1987). These authors largely follow Santesson (1952) to characterize *Gyalectidium*, adding the characteristic squamiform hyphophores. Besides the type species *G. filicinum*, they included *G. caucasicum* (Elenk. & Woron.) Vězda, formerly a synonym of *G. filicinum*, and the newly described *G. colchicum* Vězda (Vězda, 1983) and *G. eskucheii* Sérus. (Sérusiaux & De Sloover, 1986), whereas the genus *Bullatina* was established for *G. aspidotum* on account of its different hyphophores. Earlier, *G. rotuliforme* had been transferred to *Asterothyrium* (Sérusiaux & De Sloover, 1986) because of its different cortex type, simple paraphyses and absence of hyphophores.

Six further species have since been described: the foliicolous *G. palmicola* Farkas & Vězda (Farkas & Vězda, 1993), *G. imperfectum* Vězda (Vězda, 1994), *G. ciliatum* Lücking, G. Thor & Matsumoto and *G. radiatum* Lücking, G. Thor & Matsumoto (Thor, Lücking & Matsumoto, 2000), and the corticolous *G. corticola* Henssen (Henssen, 1981) and *G. yahriae* Buck & Sérus. (Buck & Sérusiaux, 2000).

The hyphophores of *Gyalectidium* were considered to be a parasymbiotic fungus by Santesson (1952); Cavalcante *et al.* (1972) described them as the imperfect genus *Tauromyces*, before Vězda (1979, 1983) correctly identified them as genuine conidiomata. Sérusiaux & De Sloover (1986) and Vězda & Poelt (1987) gave a detailed description of the anatomy and development of the hyphophores of *Gyalectidium*: they are composed of a scale or structures derived from it, with a conidia-forming layer at its base. The conidia or diahyphae are formed by branched hyphae with articulate, sausage-like cells and are always intermingled with photobiont cells. This type of hyphophore is restricted to the genus *Gyalectidium*. Together with the immersed apothecia with thalline margin and the single, muriform ascospores, the genus *Gyalectidium* seems therefore to be well circumscribed within the family Gomphillaceae, in which generic limits are otherwise uncertain and in great need of

revision (Aptroot *et al.*, 1997; Lücking 1997). The most closely related genus is *Calenia*, in which species with epithelial algae and single, muriform ascospores have recently been found (Vězda, 1979; Hartmann, 1996; Lücking, 1997), but their hyphophores are of a very different type (Vězda, 1979; Vězda & Poelt, 1987; Lücking, 1997).

In spite of the recently described species mentioned above, the genus *Gyalectidium* was generally considered to be species-poor, the only common and widespread species being *G. filicinum*, and to some extent *G. caucasicum* and *G. imperfectum*. However, recent collections gathered in all tropical areas as well as in subtropical and even such oceanic-temperate zones as Western Europe and Chile, revealed an unexpected diversity, including no less than 17 previously undescribed taxa, and forming the basis for the present survey of the genus.

MATERIAL AND METHODS

Specimens collected world-wide were studied from the following herbaria and collections: B, BM, F, G, GZU, H, LG, M, S, STU, TUR, UPS, hb. Aptroot, hb. Kalb, hb. Lücking and hb. Vězda. All anatomical observations and measurements were made in water mounts. Herbarium material for study with the scanning electron microscope (SEM) was prepared by the critical drying method.

A phenotype-based, phylogenetic analysis of *Gyalectidium* was performed as part of a comprehensive study of the Gomphillaceae (c. 260 taxa; Lücking *et al.*, in prep.). In that analysis, characters were consistently defined to produce binary (0/1) character states, which resulted in a total of 242 binary characters, divided into four main groups: (1) ecology and biogeography (33 characters), (2) thallus morphology and anatomy (46 characters), (3) apothecial morphology and anatomy (87 characters), and (4) hyphophore morphology and anatomy (76 characters). Trees were constructed by maximum parsimony using PAUP 4.0b8. The shortest trees were searched by means of heuristic search, using random stepwise addition with 100 replicates and subtree-pruning-regrafting (SPR) as branch swapping algorithm. Within-data tree stability was tested by means of a Jackknife analysis, with 1000 replicates and 10% character deletion in each replicate. To test whether alternative phylogenies are in significant conflict with the most parsimonious solutions, permutation tests were made on predefined monophyly constraints by means of ingroup taxa permutation via heuristic search on 1000 replicates.

THE GENUS *GyALECTIDIUM*

Gyalectidium Müll. Arg.

Flora 64: 100 (1881). Syn.: *Ectolechia* sect. *Gyalectidium* (Müll. Arg.) Vain., Catalogue of Welwitsch's

African Plants II: 428 (1901); *Sporopodium* sect. *Gyalectidium* (Müll. Arg.) Zahlbr. in Engler & Prantl, Die Natürlichen Pflanzenfamilien, Teil 1: 123 (1905). Type species (selected by Santesson, 1952): *G. filicinum* Müll. Arg.

Lecidea subgen. *Lopadium* sect. *Gonothecium* Vain., Acta Soc. Faun. Fl. Fenn. 7: 29 (1890). Syn.: *Sporopodium* sect. *Gonothecium* (Vain.) Zahlbr. in Engler & Prantl, Die Natürlichen Pflanzenfamilien, Teil 1: 123 (1905); *Gonothecis* Clem., The Genera of Fungi: 75, 174 (1909); *Gonothecium* (Vain.) Clem. & Shear, The Genera of Fungi: 324 (1931); *Ectolechia* sect. *Gonothecium* (Vain.) Räs., Acta Bot. Fenn. 33: 16, 57 (1943). Type species: *Lecidea phyllocharis* subsp. *glaucovirrens* Vain. = *Gyalectidium filicinum* Müll. Arg.

Cristidium R. Sant., Symb. Bot. Ups. 12(1): 357 (1952), nom. inval. [ICBN Art. 32, 36-37]. Designated type species: *Cristidium pallidum* R. Sant., nom. inval. [ICBN Art. 32, 36-37] = *Gyalectidium filicinum* Müll. Arg. (hyphophores).

Tauromyces Cavalc. & A. A. Silva in Cavalcante *et al.*, Inst. Micol. Univ. Fed. Pern. Publ. 647: 35 (1972). Type species: *Tauromyces catenulatus* Cavalc. & A. A. Silva = *Gyalectidium catenulatum* (Cavalc. & A. A. Silva) Ferraro, Sérus. & Lücking (hyphophores).

Description. Thallus foliicolous, rarely corticolous or saxicolous, crustose, usually forming small patches up to 10 mm diam., pale greenish to whitish grey, slightly nitidous, mostly encrusted with clusters of small colourless crystals of calcium oxalate giving a finely (e.g. *G. filicinum*) or coarsely verrucose surface (e.g. *G. microcarpum*), or with larger and compact aggregates of crystals forming areoles on the thallus patches (e.g. *G. areolatum*), or with the entire thallus encrusted with a continuous layer of crystals (e.g. *G. caucasicum*), or crystals lacking and then thallus smooth (e.g. *G. catenulatum*); sterile setae absent except for two species (*G. microcarpum* and *G. setiferum*); cortex always present, cartilaginous (e.g. *G. catenulatum*) or formed by a layer of rounded or elongated cells with strongly gelatinized walls (e.g. *G. filicinum*). Photobiont a species of *Trebouxia* (Chlorococcaceae), with rounded green cells.

Hyphophores (Figs 1–4) often present, in most species composed of an upright, oblique or horizontal scale [per definition, the width of the scale is the dimension of its line of attachment to the thallus and its length is the perpendicular dimension], pale grey or whitish, rarely ± dark bluish, dark grey, or even black (*G. atrosquamulatum*), with its upper parts blunt, irregularly incised (e.g. *G. caucasicum*), dentate (e.g. *G. palmicola*) or provided with two acute appendages (e.g. *G. filicinum*); scale sometimes absent (*G. membranaceum*), reduced and membranaceous (*G. imperfectum*), translucent, lacinate (e.g. *G. laciniatum*),

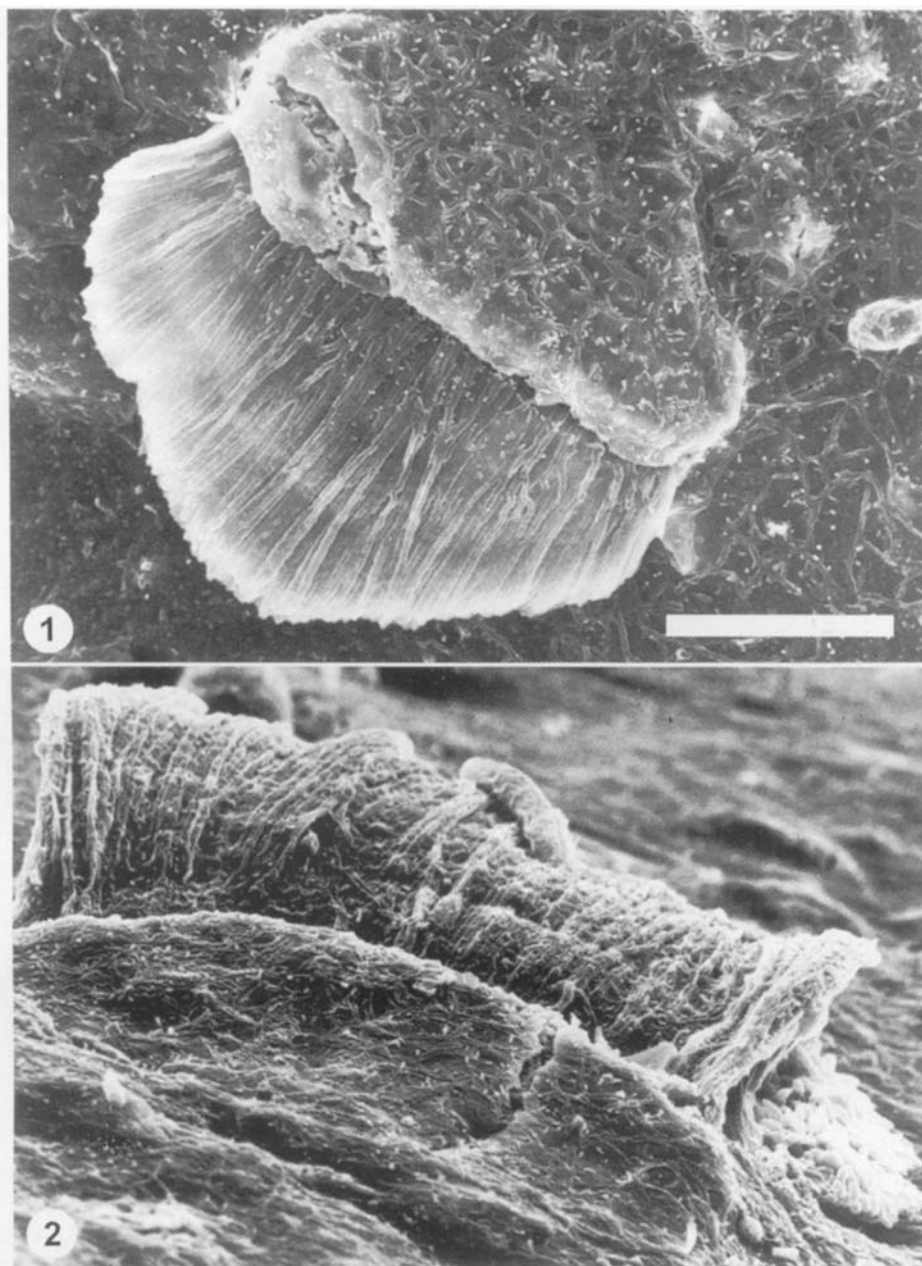
transformed into single, marginal cilia (*G. ciliatum*) or a circle of several ones (*G. eskucheii* and *G. setiferum*), bordering concave, crater-like depressions (*G. denticulatum* and *G. kenyanum*), or looking like flower vases with a dentate edge (*G. yahriae*). Diahyphae (Figs 5, 6) forming the so-called ‘diahyphal mass’ or ‘conidial mass’ produced at the base of the scale, or underneath it when the scale remains horizontal, or at its centre when the hyphophore has a radial symmetry, formed by branched, articulate hyphae with sausage-shaped cells and always associated with small algal cells, or rarely made of drop-like cells with the outer ones developing long cilia (*G. yahriae*). Mass of diahyphae usually individualizing into smaller and rounded masses that act as single diaspores and disperse both bionts together.

Apothecia present or absent, in some species mostly present on thalli not producing hyphophores, 1–10 per thallus patch, isolated in most species but contiguous and sometimes even aggregated (e.g. *G. catenulatum*), immersed in the thallus but erumpent, rounded or rarely irregular and polygonal or even lobed to lir-elliform (*G. filicinum*), with a thalline margin; disc usually yellowish green or greyish, rarely covered by a brownish pigment (*G. fuscum*), especially when young, whitish pruinose in a few species (*G. microcarpum*); margin slightly prominent, of the same colour as the surrounding thallus or paler, or with the same brownish pigment as on the disc surface (*G. fuscum*); in old apothecia a narrow fissure often separating the margin from the disc (e.g. *G. microcarpum*). Proper exciple strongly reduced, prosoplectenchymatous, laterally covered by algiferous thallus tissue encrusted with crystals. Epithecium including numerous algal cells smaller than those of the thallus. Hymenium non-amyloid, colourless. Paraphyses abundant, 0.7–1.0 µm thick, richly branched and anastomosing. Asci broadly clavate to ovoid, non-amyloid, of the annelascaceous type, i.e. with a ring-shaped structure when young, in the mature condition typically thin-walled and completely filled by the ascospore. Ascospores single in the ascus, oblong-ellipsoid to ovoid, richly muriform, colourless.

Pycnidia known in a single species (*G. colchicum*), seen as dark bluish spots slightly raised on the thallus surface; conidia bacilliform to slightly bifusiform, 2–3 × 0.75 µm.

Systematic relationships

The genus *Gyalectidium* clearly belongs to the family Gomphillaceae, currently placed in the order Ostropales (Lücking 1997). With the Ostropales, it shares the hemiangiocarpous apothecial development, the non-amyloid hymenium, and the ‘annelascaceous’ ascus type, and with the Gomphillaceae, the branched and

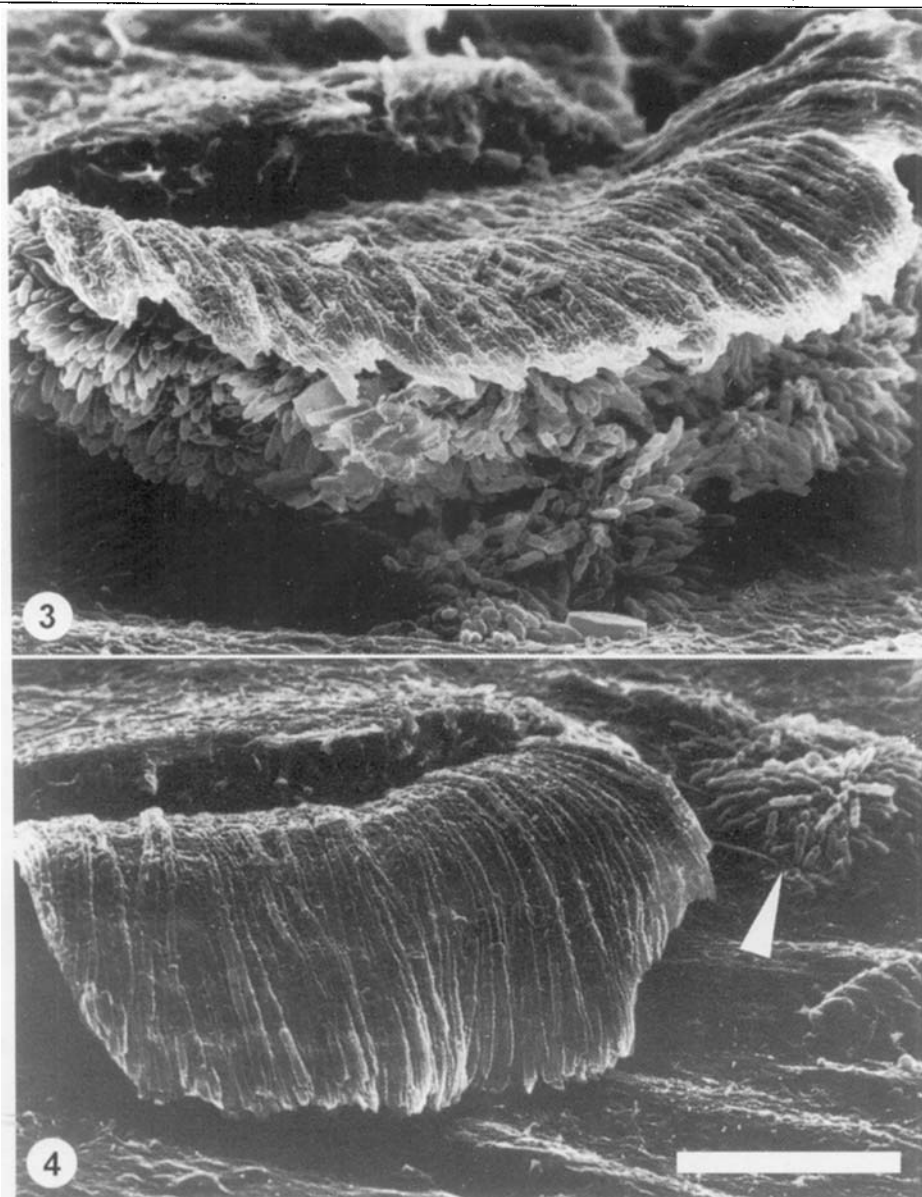


Figures 1, 2. Hyphophores of *Gyalectidium flabellatum* (holotype), seen from above and from behind. Scale bar = 50 μ m.

anastomosing paraphyses and the highly specialized conidiomata named hyphophores. Within the Gomphillaceae, three other genera, viz. *Calenia*, *Caleniopsis*, and *Bullatina*, share the same apothecium type (Santesson 1952; Vězda & Poelt 1987; Lücking 1997). In both *Calenia* and *Bullatina*, epithelial algae and single, muriform ascospores are known, but the hyphophore type is clearly different in being setiform and producing the masses of diahyphae (sub)apically. Hyphophores that are superficially similar to those of *Gyalectidium* are known only in a few species of the

highly variable and heterogenous genus *Gyalideopsis* (Lücking, 1999) and the recently described *Hippocrepidea nigra* Sérus. (Aptroot *et al.*, 1997). However, the internal anatomy of the hyphophores and the structure of the diahyphae in these species is quite different from those of *Gyalectidium*, clearly indicating that convergent evolution is involved.

Based on a forthcoming phenotype-based phylogenetic analysis of the Gomphillaceae (Lücking *et al.*, in prep.), the genus *Gyalectidium* is derived from *Calenia*, which in turn seems to be derived from *Gyalideopsis*,



Figures 3, 4. Hyphophores of *Gyalectidium flabellatum* (holotype), fully mature (3) and postmature (4) with extruded diahyphae (arrow). Scale bar = 50 μ m.

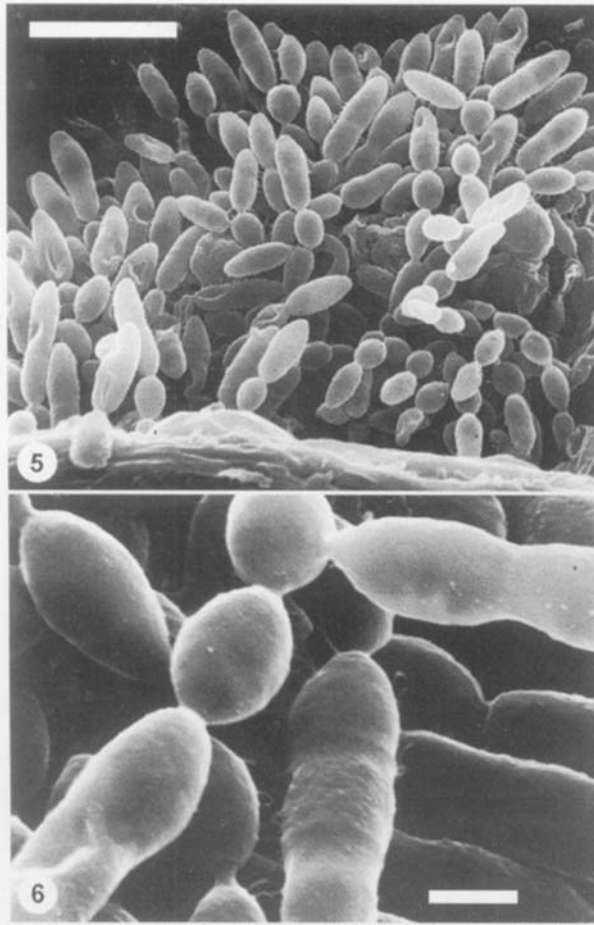
and not from *Echinoplaca* as previously assumed (Lücking, 1997). The particular squamiform hyphophores would then have evolved from the setiform type. *Calenia lueckingii* Hartmann (Hartmann, 1996) and *C. monospora* Vězda (Vězda, 1979) would then be intermediate between both genera, and indeed, both appear as such in the phylogram (Fig. 7).

Infrageneric classification

Within the genus, the morphological features suggest the distinction of three groups, which are supported by the phenotype-based phylogenetic analysis (Fig. 8):

a group centred around *Gyalectidium caucasicum* (*G. caucasicum* group), another centred around *G. areolatum* (*G. areolatum* group), and a third one centred around *G. filicinum* (*G. filicinum* group).

The species of the *Gyalectidium caucasicum* group are characterized by thalli strongly and evenly encrusted with calcium oxalate crystals. The thallus patches therefore appear silvery grey to whitish and usually inflated to almost bullate. There is a clear tendency towards producing the hyphophores at the thallus margin, with the scales being often reduced, as can be observed in the "row" formed by *G. caucasicum*, *G. minus*, *G. flabellatum*, *G. australe*,



Figures 5, 6. Diahyphal mass of *Gyalectidium flabellatum* (holotype) in different magnification, showing branched filaments with sausage-shaped cells (5) and details of the isthmi (6). Scale in (5) = 10 μm , in (6) = 2 μm .

G. maracae, *G. novoguineense*, and *G. ciliatum*. In the phenotype-based phylogenetic analysis with three selected species of *Calenia* as outgroup, the *G. caucasicum* group always comes at the base of the tree as a paraphyletic entity. Whether this actually reflects a true plesiomorphic position within the genus is open to question, but it is confirmed by the fact that the species of this group usually have a cartilaginous cortex typical of *Calenia* and other genera in the Gomphillaceae, and different from the cellular cortex in the *Gyalectidium filicinum* group.

The *Gyalectidium areolatum* group includes species with smooth thallus lacking crystals (*G. catenulatum*) or taxa with areolate thalli, i.e. whitish crystalline areoles separated and surrounded by non-crystalline, greenish areas (*G. areolatum*). This group is in many respects intermediate between the *G. caucasicum* and *G. filicinum* group, which is reflected by its position in the phylogram (Fig. 8). For example, while there is

a tendency towards marginal formation of the hyphophores, their scales are mostly well-developed and large, resembling those of *G. filicinum*.

The *Gyalectidium filicinum* group itself takes an apical position in the phylogram and thus appears monophyletic. It is characterized by a finely verrucose thallus, the calcium oxalate crystals being aggregated in small, wart-shaped agglomerations. In addition, a cellular cortex is usually present. The hyphophores are mostly formed on the thallus surface but often near the margins. There is a high variability in the development and shape of the scale, being well-developed in *G. filicinum*, irregularly dissected in *G. laciniatum*, dissolved into individual setae in *G. eskuichei*, or absent in *G. imperfectum*.

It is interesting to note that, at least on the basis of the analysis of the phenotype, the characters of the thallus (distribution of crystals and formation of a cellular cortex) are decisive in determining phylogenetic relationships, while the structure of the hyphophores is not. Hyphophores of a similar type can be found in distantly related taxa while closely related species, such as *G. filicinum* and *G. imperfectum*, differ considerably in the morphology of their hyphophores. Ecological studies indicate that most species of the genus are rather similar in their ecological preferences, in spite of their different thallus morphology, and hence, thallus features are likely to have been fixed early after initial evolutionary radiation as compared to hyphophore structure.

Although a phenotype-based phylogenetic study can only create hypotheses about evolutionary relationships within the genus, the rather robust structure of the trees and the correlation with certain 'key' characters allows, in our eyes, formal recognition of the different groups at subgeneric level. This is also done in the light of current splitting of genera into smallest entities, to alternatively demonstrate how a group can be formally structured without such splitting and respective name changes. In doing so, we also accept paraphyletic groups as natural, especially since introducing monophyletic constraints for the groups in question would make the resulting most parsimonious trees (Fig. 9) only insignificantly longer (length difference = 5 steps/1.8%, $P < 0.01$).

Following principles that are outlined in an integrative study on Gomphillaceae (Lücking, Sérusiaux & Vězda, in prep.), and adopting provisions made by the International Code of Botanical Nomenclature, we formally recognize the three major groups at the sectional level, each one with a single series (Fig. 9, Table 1). In addition, two further species that appear isolated from these groups are placed into monotypic sections and series, viz. *Gyalectidium microcarpum*, because of its coarsely verrucose thallus with abundant sterile setae but lacking hyphophores, and *G. yahriae*,

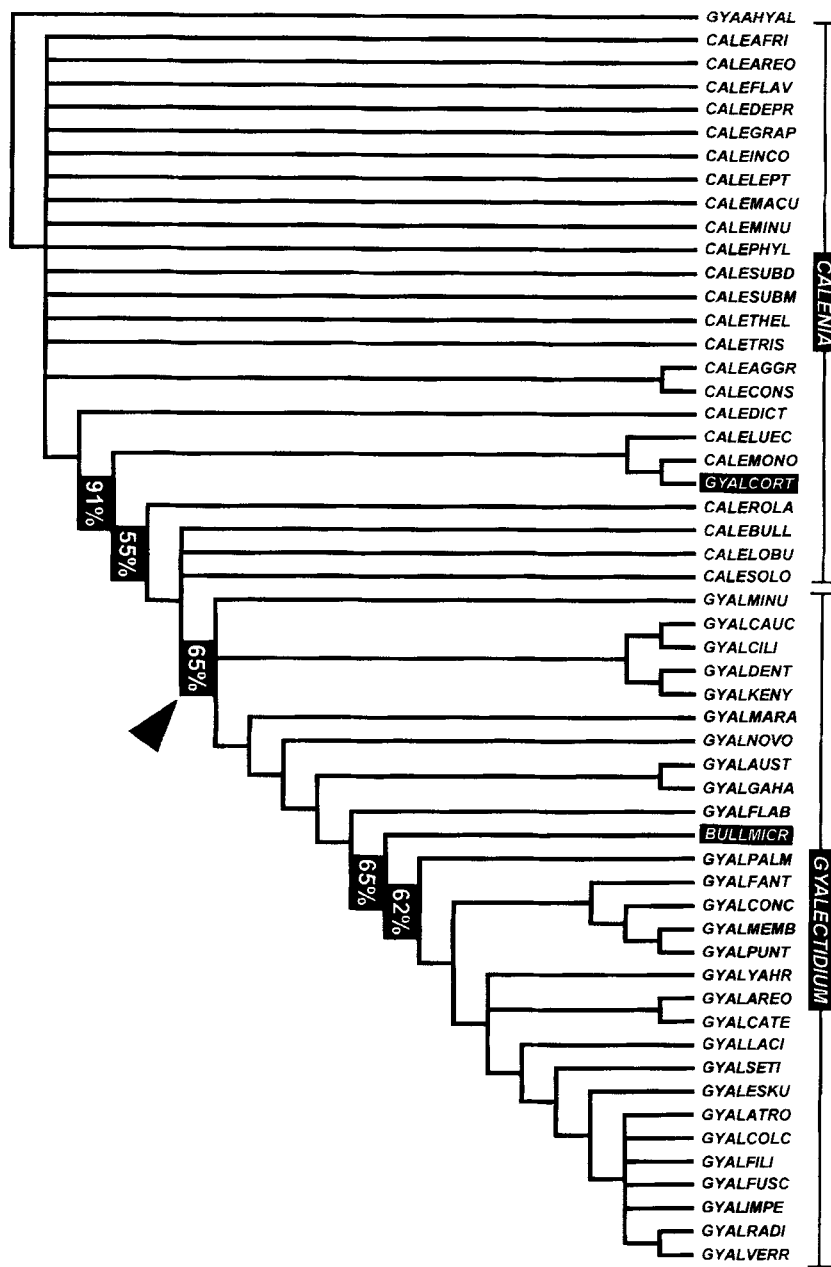


Figure 7. Strict consensus of 5616 equally parsimonious trees (528 steps) of species currently assigned to *Calenia* and *Gyalectidium* [including *Bullatina microcarpa* (= *Gyalectidium microcarpum*)], based on a phylogenetic analysis of 242 binary phenotype characters (no weights and ancestral state definitions applied; trees rooted with outgroup *Gyalidea hyalinescens* Vezda). Jackknife values relating to the most important bipartitions within the tree are indicated, the arrow pointing to the division of *Calenia* and *Gyalectidium* (setiform vs squamiform hyphophores). Note that *Calenia* forms a paraphyletic residual which confirms its basal position against *Gyalectidium*, and that *Gyalectidium corticola* and *Bullatina microcarpa* (highlighted) fall within *Calenia* and *Gyalectidium*, respectively (after Lücking *et al.*, in prep.).

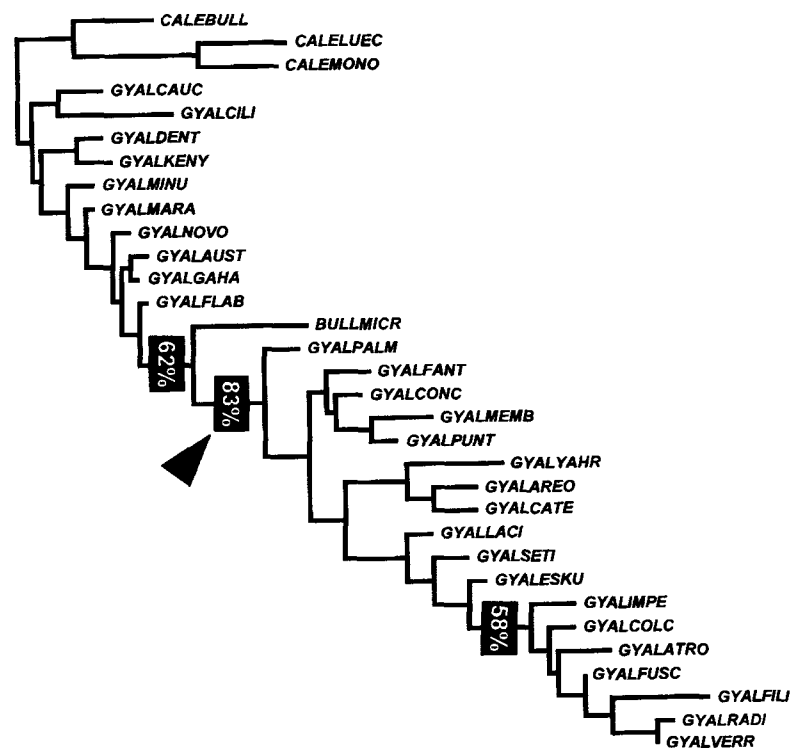


Figure 8. One out of six equally parsimonious trees (272 steps) of *Gyalectidium* [including *Bullatina microcarpa* (= *Gyalectidium microcarpum*)], based on a phylogenetic analysis of 242 binary phenotype characters (no weights and ancestral state definitions applied; trees rooted with outgroup *Calenia bullatinoides* Lücking, *C. lueckingii* Hartmann and *C. monospora* Vězda). Jackknife values relating to the most important bipartitions within the tree are indicated, the arrow pointing to the division of the *Gyalectidium areolatum* vs the *G. caucasicum* group, with *Bullatina microcarpa* (= *Gyalectidium microcarpum*) as intercalary taxon. Note the basal position of the *G. caucasicum* group, although the outgroup includes taxa that represent the thallus morphology found in all three major groups of *Gyalectidium* (placoid-bullate, smooth, and finely verrucose).

because of its modified hyphophores that functionally resemble goniocystangia and soralia. This requires formal description of the following four new sections (each one with a single series), in addition to the autonomous sect. *Gyalectidium* ser. *Gyalectidium* (the *G. filicinum* group), that includes the type species of the genus.

Gyalectidium* sect. *Placolectidium* ser. *Caucasicae
Lücking, Sérus. & Vězda sect. et ser. nov.

Sectione *Gyalectidio* seriei *Gyalectidio* thallo placodioido vel bullato crystallis aequaliter insperso cortice cartilagineo instructo differt. Hypophori plerumque in margine thallorum formati, squamae saepe diminutae. Typus sectionis et series: *Gyalectidium caucasicum* (Elenk. & Woron.) Vězda (holotypus).

The name of this section is a combination of the adjective 'placodioidus' (referring to the characteristic thallus morphology) and the generic name *Gyalectidium*.

Gyalectidium* sect. *Areolectidium* ser. *Areolatae
Lücking, Sérus. & Vězda sect. et ser. nov.

Sectione *Gyalectidio* seriei *Gyalectidio* thallo areolato vel laevigato crystallis aggregatis vel ausentis cortice cartilagineo instructo differt. Hypophori in lamina vel margine thallorum formati, squamae bene evolutae vel raro diminutae. Typus sectionis et series: *Gyalectidium areolatum* Ferraro & Lücking (holotypus).

The name of this section is a combination of the adjective 'areolatus' (referring to the characteristic morphology of the type species) and the generic name *Gyalectidium*.

Gyalectidium* sect. *Setolectidium* ser. *Microcarpae
Lücking, Sérus. & Vězda sect. et ser. nov.

Sectione *Gyalectidio* seriei *Gyalectidio* thallo grosse verrucoso setis sterilis et cortice cartilagineo instructo differt. Hypophori deficientes. Typus sectionis et series ad huc species unica: *Gyalectidium microcarpum* (Vězda) Lücking, Sérus. & Vězda (holotypus).

The name of this monotypic section is a combination

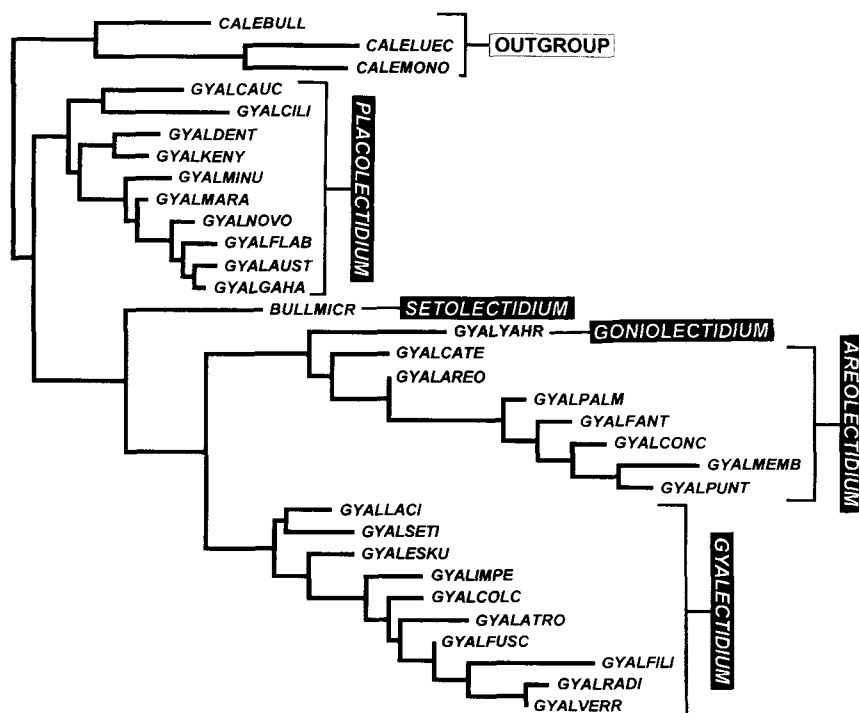


Figure 9. One out of 42 equally parsimonious trees (277 steps) of *Gyalectidium* [including *Bullatina microcarpa* (= *Gyalectidium microcarpum*)], based on a phylogenetic analysis of 242 binary phenotype characters (no weights and ancestral state definitions applied; trees rooted with outgroup *Calenia bullatinoidea* Lücking, *C. lueckingii* Hartmann and *C. monospora* Vězda), introducing monophyletic constraints for the five sections suggested to be formally recognized within the genus. The trees are not significantly longer than those derived without applying monophyletic constraints (permutation test: tree length difference = 5 steps/1.8%, $P < 0.01$).

of the word 'seta' (the section includes the only species with genuine sterile setae) and the generic name *Gyalectidium*.

Gyalectidium* sect. *Gonioelectidium* ser. *Yahriae

Lücking, Sérus. & Vězda sect. et ser. nov.

Sectione *Gyalectidio* seriei *Gyalectidio* thallo laevigato cortice cartilagineo instructo differt. Hypophori ex squamis pluris compositi, goniocystangii similes. Typus sectionis et series ad huc species unica: *Gyalectidium yahriae* Buck & Sérus. (holotypus).

The name of this monotypic section is a combination of the term 'goniocystangium' (referring to the functional similarity of the hyphophores with goniocystangia) and the generic name *Gyalectidium*.

The systematic arrangement of all 29 currently accepted species in the genus and included in this monograph among the sections and series described above is outlined in Table 1.

Notes on the hyphophores

It is now generally accepted that hyphophores are conidiomata, and particularly modified synnemata.

Their sterile parts are indeed rather rigid and permanent (at least they survive as long as the lichen thallus on which they grow) and the so-called 'diahypal mass' or 'conidial mass' (diahypae) is analogous to genuine conidia. In most species of the Gomphillaceae and most probably in all species of *Gyalectidium*, the conidial mass usually breaks down into smaller and rounded masses which represent single diaspores and disperse both bionts together; turgescence of the masses of diahyphae during wet periods, retraction during desiccation and any mechanical agencies (small animals, water droplets, etc.) being the passive means of dispersal. The only notable exception is *G. membranaceum*, in which the whole structure (the conidial mass together with the membranaceous upper layer) acts as a single diaspore.

Following the terminology of Minter *et al.* (1982, 1983), Sérusiaux & De Sloover (1986) described the pattern of development of the diahyphae in several species of the Gomphillaceae (species of *Gyalectidium* ssp. and *Tricharia armata*). They assumed that diahyphae are conidia that develop with the following pattern: holoblastic conidial ontogeny, replacement of wall building apex at one or two loci, maturation by

Table 1. Formal systematic subdivision of the genus *Gyalectidium*

Genus *Gyalectidium* Müll. Arg.
 Subgenus *Gyalectidium* (autonomous)
 Sectio *Placogyalectidium* Lücking, Sérus. & Vězda
 Series *Caucasicae* Lücking, Sérus. & Vězda
G. australe Lücking
G. caucasicum (Elenk. & Woron.) Vězda
G. ciliatum G. 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.
 Sectio *Setolectidium* Lücking, Sérus. & Vězda
 Series *Microcarpae* Lücking, Sérus. & Vězda
G. microcarpum (Vězda) Lücking, Sérus. & Vězda
 Sectio *Goniolectidium* Lücking, Sérus. & Vězda
 Series *Yahriae* Lücking, Sérus. & Vězda
G. yahriae Buck & Sérus.
 Sectio *Areogyalectidium* Lücking, Sérus. & Vězda
 Series *Areolatae* Lücking, Sérus. & Vězda
G. areolatum Ferraro & Lücking
G. catenulatum (Cavalc. & A. A. Silva) Ferraro, Lücking & Sérus.
G. conchiferum Lücking & Wirth
G. fantasticum Ferraro & Lücking
G. membranaceum Sérus. & Lücking
G. palmicola Farkas & Vězda
G. puntilloi Sérus.
 Sectio *Gyalectidium* (autonomous)
 Series *Gyalectidium* (autonomous)
G. atrosquamulatum Lücking & Kalb
G. colchicum Vězda
G. eskucheii Sérus.
G. filicinum Müll. Arg.
G. fuscum Lücking & Sérus.
G. imperfectum Vězda
G. laciniatum Lücking
G. radiatum G. Thor, Lücking & Matsumoto
G. setiferum Vězda & Sérus.
G. verruculosum Sérus.

diffuse wall building, delimitation by transverse septa, perhaps sometimes incomplete or very slow to appear; occasionally lateral holoblastic ontogeny occurs on the conidiogenous hyphae much lower down than the building apices and thus long chains of conidia are produced. This hypothesis has never been tested or examined in detail, and Sérusiaux (1998) has suggested another pattern. While searching for fungi producing similar (either analogous or homologous) conidiomata, he

found several genera of hyphomycetes, such as *Speiroopsis scopiformis* Kuthub. & Nanawi and *Wiesneriomyces conjunctosporus* Kuthub. & Nanawi, growing on bark or on leaves immersed in water in tropical areas. In these taxa, conidia are blastic, sometimes branched, and without septa but with regularly-spaced constrictions (isthmi), are produced in acropetal succession, and the conidiogenous cells proliferate sympodially. This development pattern is consistent with the observations made in the Gomphillaceae, and especially with *Gyalectidium*. By all means, the genuine identity of the diahyphae forming the conidial mass and their development pattern require further studies which are beyond the scope of the present paper.

The results presented in this paper lead to some corrections of those of Sérusiaux & De Sloover (1986) obtained on collections from northern Argentina and adjacent Brazil (Foz de Iguazú). Indeed, besides the fact that the populations they identified as *Gyalectidium filicinum* represent *G. areolatum* or *G. catenulatum*, the hyphophore development presented for *G. eskucheii* was actually based on mixed collections of that species and *G. imperfectum* (a species not recognized at that time). These authors assumed that the horizontal scale typical of the latter represents the immature stage of the former. Our studies, based on much larger collections, demonstrate that the scales of *G. imperfectum* remain horizontal when mature, and that cilia can develop even on their outer edges in certain, probably rather xeric, conditions. In summary, the collections studied by Sérusiaux & De Sloover (1986) contain four *Gyalectidium* species: *G. areolatum*, *G. catenulatum*, *G. eskucheii* (holotype) and *G. imperfectum*.

Ecogeography

As *Gyalectidium corticola* is excluded from the genus (see below), the only typically corticolous species of *Gyalectidium* is thus *G. yahriae*, known from twigs and decorticated wood in Florida and in the mountains of Papua New Guinea. It is also the only species with conidial masses formed by cells that are quite short and look like 'strings of beads', with cilia developing on many of the outer cells. All other species are considered as strictly foliicolous. One should however keep in mind that the highly specialized ecological niche formed by rocks at water level along streams can shelter species of the Gomphillaceae, amongst which *Gyalectidium* can be found. Only one such case is so far reported (*G. filicinum*; Sérusiaux, 1998) but we expect that more detailed exploration of this habitat will yield further reports.

The recent discovery of so many new species in the genus suggests that it is probably undercollected, or specimens have been mistaken for the common *G.*

filicinum or *G. caucasicum*. Indeed, the often very tiny hyphophores that characterize several species with an otherwise identical thallus morphology are quite easily overlooked. Any discussion on distribution patterns and ecological requirements for most species is therefore preliminary. However, it can be stated that *G. filicinum* is by far the most common and widespread representative of the genus. It appears in nearly each set of foliicolous lichens gathered in tropical areas and has a wide ecological amplitude: it can be found from lowland to upper montane rain forest, in primary as well as in secondary and anthropogenic vegetation, and in the shady understorey as well as in the exposed upper canopy (Lücking, 1997). However, the species is most frequently found in natural light gaps within the forest or at semi-exposed forest margins. *Gyalectidium filicinum* seems also to prefer areas with high precipitation, such as Costa Rica and Cocos Island (Lücking & Lücking, 1995), while in the continental lowland forests of South America and Africa it is less common. With its small thallus and frequent hyphophores, it is a typical 'pioneer' species and appears very early on young leaves, together with *Phyllophiale alba* R. Sant. and *Coenogonium subluteum* (Rehm) Kalb & Lücking [= *Dimerella epiphylla* (Müll. Arg.) Malme] (Lücking, 1998), but persists even in old leaves, densely covered with lichens.

Up to seven *Gyalectidium* species frequently occur together on the same leaves suggesting that the species have similar ecological needs. Some differentiation can be found, however, in species such as *G. catenulatum* or *G. caucasicum*, which prefer more open situations. *G. catenulatum* seems to be a typical canopy dweller and is usually not found in the forest understorey, while *G. caucasicum* is more likely to be detected in open secondary vegetation. Several species are thus far known from only a few collections, so that generalizations about their ecology are impossible at present.

The distribution of the species (Table 2) shows no clear pattern between and within the two main species groups circumscribed above (*Gyalectidium filicinum* and *G. caucasicum* groups). The high diversity of species, especially in South America (Costa Rica, Argentina and adjacent areas), Europe, and Australasia, is remarkable but most probably a result of the recent collecting efforts in these areas. Asia is undercollected as virtually no extensive collections of foliicolous lichens are available from its large tropical areas, especially Indochina and Indonesia.

The Neotropics have the highest number of species, especially Costa Rica. This is no surprise as that country has been intensively explored by one of us. However, the abundance and diversity in northern Argentina and adjacent Paraguay and Brazil are remarkable, although no species is endemic to this area.

Table 2. World distribution of species of *Gyalectidium*. AM = Tropical America (southern USA to northern Chile and Argentina), AF = Tropical Africa, EU = Europe, Caucasus and Macaronesia, AS = Asia and Australasia (including Malesia and Australia with western Pacific islands)

	AM	AF	EU	AS
<i>G. areolatum</i>	+	-	-	-
<i>G. atosquamulatum</i>	-	+	-	-
<i>G. australe</i>	-	-	-	+
<i>G. catenulatum</i>	+	-	-	-
<i>G. caucasicum</i>	+	+	+	+
<i>G. ciliatum</i>	+	+	-	+
<i>G. colchicum</i>	-	-	+	-
<i>G. conchiferum</i>	+	-	-	-
<i>G. denticulatum</i>	+	-	-	-
<i>G. eskucheii</i>	+	+	-	-
<i>G. fantasticum</i>	+	-	-	-
<i>G. filicinum</i>	+	+	-	+
<i>G. flabellatum</i>	-	-	-	+
<i>G. fuscum</i>	-	+	-	+
<i>G. gahavisukanum</i>	-	-	-	+
<i>G. imperfectum</i>	+	+	-	+
<i>G. kenyanum</i>	-	+	-	-
<i>G. laciniatum</i>	+	-	-	-
<i>G. maracae</i>	+	-	-	-
<i>G. membranaceum</i>	-	-	+	-
<i>G. microcarpum</i>	-	+	-	+
<i>G. minus</i>	-	-	+	-
<i>G. novoguineense</i>	-	-	-	+
<i>G. palmicola</i>	+	-	-	-
<i>G. puntilloi</i>	-	-	+	-
<i>G. radiatum</i>	-	-	-	+
<i>G. setiferum</i>	-	-	+	-
<i>G. verruculosum</i>	-	-	-	+
<i>G. yahrae</i>	+	-	-	+
Total	14	9	6	13

It is worth notice that, although the Neotropics are comparatively well-explored, several species are known only from a single collection (*G. conchiferum*, *G. denticulatum*, *G. laciniatum*, and *G. palmicola*, the last being known only from a botanical garden).

It is of interest that six species are now known from Europe (including the Caucasus and Macaronesia) with several interesting patterns and a strong endemism: *Gyalectidium membranaceum* is endemic to an island of the Canary Islands, *G. puntilloi* to the Pyrenees and southern Italy, *G. colchicum* to the western Caucasus and Macaronesia, *G. setiferum* to the western Caucasus and south-west Europe, and *G. minus* to south-west Europe and the Canary Islands.

Africa is quite poor in *Gyalectidium* species but two

recently discovered species in Kenya (*G. atosquamulatum* and *G. kenyanum*, both known from the same, single locality) may indicate that that continent is still undercollected.

Finally, several species of Australasia have classic distribution patterns, as a rule being present in Papua New Guinea and/or Australia and/or islands of the south-western Pacific (*G. australe*, *G. gahavisukanum*, *G. flabellatum*, *G. novoguineense*, *G. radiatum* and *G. verruculosum*). Whether the remarkable occurrence of *G. microcarpum* in southern Africa and Australasia represents a genuine southern hemisphere distribution is open to question, as such a pattern, commonly found among vascular plants, is rare in foliicolous lichens.

TAXONOMIC ACCOUNT

In the following account, species are listed in alphabetical order; their systematic arrangement is presented in Table 1. Illustrations do not follow alphabetical order but their systematic relationship to facilitate comparison. Nomenclatural references and synonymy are given in full with notes on taxonomy, distribution and ecology.

Gyalectidium areolatum Ferraro & Lücking sp. nov.

(Fig. 20)

A *Gyalectidio filicino* thallo areolato et hyphophoribus, late squamiformibus, in margine areolarum formatis differt. Typus: ARGENTINA. Formosa: Estancia Guaycolec, 1995, Ferraro *et al.* 5304 (CTES, holotypus).

Description. THALLUS forming rounded patches 1–3 mm diam., distinctly areolate, with whitish, applanate, polygonal crystalline clusters separated or surrounded by thin greenish thallus parts, areoles usually first formed at the centre, becoming confluent in well-developed thalli. HYPHOPHORES submarginal, their scales well developed, emerging on the outer edge of crescent-shaped areoles, obliquely orientated, squamiform and usually with two acute, lateral projections, 0.2–0.5 mm broad and 0.15–0.2 mm long, whitish translucent to pale yellowish to orange, or greyish. APOTHECIA rare but abundant on thalli that produce them, sometimes arranged in a circle near the margin, rounded but sometimes confluent, 0.1–0.2 mm diam., with greyish brown disc and margin. ASCOSPORES ellipsoid, 35–45 × 12–18 µm. PYCNIDIA not found.

Notes. This new species is easily recognized by the combination of an areolate thallus and broadly squamiform hyphophores that originate on the outer edge of crystalline areoles. Mature hyphophores are similar to those of *Gyalectidium filicinum*, but their connection to crystalline areoles and their ontogeny underline

the intermediate position towards the *G. caucasicum* group. The very young hyphophores project horizontally from the margins of the areoles, and only during their later development do they turn upright. The thallus areoles are widely separated by thin, greenish thallus areas without crystals, which might be the reason why the hyphophores are finally located on the thallus surface. A similar thallus morphology is known from the Cuban *G. palmicola*, which has marginal hyphophores with shorter, horizontally orientated, dentate scales, and the south-west European *G. puntilloi*, in which the hyphophore scales are usually distorted, lacerated and reduced to clusters of membranaceous lobes, pale greyish or whitish, sometimes with a bluish tinge at their base.

Distribution and ecology. *Gyalectidium areolatum* is known from various parts in the Neotropics but seems to be most common in northern Argentina and adjacent Paraguay. Its ecology is rather similar to that of *G. filicinum* but it seems to prefer somewhat more open situations.

Additional specimens examined. MEXICO. Unknown locality, 1980, Roskoski s.n. (LG). BRAZIL. São Paulo: between Ubatuba and Paratí, 23°20'S, 45°00'W, sea level, 1979, Kalb & Plöbst s.n. (hb. Kalb). Botukatu, 22°50'S, 46°25'W, 850 m, 1979, Kalb & Gottsberger s.n. (hb. Kalb). PARAGUAY. Caazapá: Yuty District, 15 km south of Capitindy, 1987, Arbo 2922 (CTES). Amambay: 7 km north of ruta 5, west limit of Cerro Corá National Park, 1988, Ferraro *et al.* 3466 (CTES). Alto Paraná: Biological Reserve near Itabó river, 54°5'S, 25°5'S, 1996, Schinini *et al.* (CTES). Canendiyú, 22 km of Colonia Nueva Esperanza, Itabó Private Reserve, 24°35'S, 54°48'W, 260 m, 1996, Schinini *et al.* 31567 (CTES). ARGENTINA. Corrientes: Depto. Capital, Riachuelo, 1996, Ferraro 5317, 5320 (CTES); *ibid.*, 6 km SW of Colonia Garabí, 1982, Tressens *et al.* 2135 (CTES). Formosa: Depto. Capital, Estancia Guaycolec, 1995, Ferraro *et al.* 5294, 5302, 5309 (CTES, topotypes). Depto. Santo Tomé, 3 km south-west of Gobernador Virasoro, 1982, Tressens 2126 (CTES). Misiones: Depto. Guaraní, 1500 m, 1994, Maruñak 729, 744, 777 (CTES), 735 (hb. Lücking). Predio Guaraní, 1995, Tressens *et al.* 5511 (CTES). Depto. Iguazú, Iguazú National Park, 1995, Maruñak *et al.* 871 (CTES); *ibid.*, 1995, Vanni *et al.* 3503 (CTES). CHILE. Los Lagos: Choshuenco, Volcán El Mocho, 600–630 m, 1999, Wirth & Feuerer 33906 (STU).

Gyalectidium atosquamulatum Lücking & Kalb

sp. nov.

(Fig. 15)

A *Gyalectidio imperfecto* hyphophoribus liguliformibus nigris differt. Typus: KENYA. Eastern Province: Ma-

KEY TO THE SPECIES OF *Gyalectidium*

- 1 Thallus coarsely but regularly verrucose, with sterile setae (= setae not associated with the production of diahyphae) dispersed over the whole thallus surface; hyphophores unknown (Southern Africa and Australasia) *G. microcarpum*
- 1* Thallus smooth, or finely verrucose, or areolate, or areolate-bullate, without sterile setae or rarely (*G. setiferum*) with few sterile setae associated with setose hyphophores 2
- 2 Thallus corticolous; hyphophores looking like flower vases with a dentate edge; diahyphal mass clearly dividing into smaller entities, the diahyphal cells rounded and most of the outer ones producing a long cilium (Florida, USA and Papua New Guinea) *G. yahrae*
- 2* Thallus foliicolous, or very rarely on rocks at water level along streams; hyphophores of various shapes but not as above; diahyphal mass dividing into smaller entities only when squashed in microscopic preparation, the diahyphal cells sausage-shaped and never producing cilia 3
- 3 Hyphophore scales, for most of their length or entirely, divided into narrowly triangular lobes or groups of individual setae; hyphophores laminal 4
- 3* Hyphophore scales entire or incised at their tips, rarely reduced or absent, with two acute lateral projections in some species, if setiform then marginal 8
- 4 Thallus areolate-bullate, silvery grey; diahyphal mass immersed into a circular, crater-like depression, their margin provided with several teeth-shaped setae pointing towards the centre 5
- 4* Thallus finely verrucose to almost smooth, greenish grey; diahyphal mass superficial or partly surrounded by a crystalline bulge 6
- 5 Diahyphal mass with a green surface; surrounding setae 0.05–0.1 mm long, and thus usually smaller than the depression diameter (Costa Rica) *G. denticulatum*
- 5* Diahyphal mass with a greyish surface; surrounding setae 0.1–0.3 mm long, and thus usually longer than the depression diameter (Kenya) *G. kenyanum*
- 6 Hyphophore scales for most of their length divided into irregular, narrowly triangular lobes, basally confluent and usually immersed into a semicircular, crystalline bulge (Costa Rica) *G. laciniatum*
- 6* Hyphophore scales entirely divided into groups of individual setae that emerge from or surround the diahyphal mass; crystalline bulge absent or ring-shaped 7
[If thallus almost smooth, not finely verrucose, and provided with few, rather large hyphophores, see *Gyalectidium* sp. A]
- 7 Diahyphal mass raised over the thallus surface, yellowish green, slightly translucent, surrounded by individual setae; additional sterile setae irregularly dispersed over the thallus surface (west Caucasus and western Europe) *G. setiferum*
- 7* Diahyphal mass adnate to the thallus surface, forming a dark greyish brown spot from which a circle of setae or narrowly triangular lobes emerges; additional sterile setae absent. South America and Southern Africa *G. eskucheii*
- 8 Thallus greenish, usually lacking crystals and completely smooth, or with very few, scattered verrucae 9
- 8* Thallus greenish or silvery grey, encrusted with crystals, finely verrucose, or areolate, or areolate-bullate 10
- 9 Hyphophores laminal, their scales basally straight or cucullate, with two long, acute, lateral projections (Tropical America) *G. catenulatum*
- 9* Hyphophores marginal, their scales basally bent inwards and with entire margins (Chile)
..... *G. conchiferum*
- 10 Hyphophore scale reduced and membranaceous, or absent; diahyphal mass usually visible as a bluish grey to dark greyish brown, reniform spot on the thallus or at the margin 11
- 10* Hyphophore scale well developed but sometimes small and rather inconspicuous 12
- 11 Thallus thin but usually with a crystal areole in the centre; hyphophores without any distinct scale, and thus reduced to a thin diahyphal mass, often detached and leaving a distinct marginal scar which gives the thallus a crenate margin (Canary Islands: La Palma) *G. membranaceum*
- 11* Thallus well developed, finely verrucose; hyphophores usually persistent, forming a dark greyish brown spot on the thallus surface or at the margin, sometimes with an membranaceous, laciniate scale or slightly erect hairs on its outer edge (Pantropical) *G. imperfectum*

continued

KEY TO THE SPECIES OF *GYALECTIDIUM* – continued

- 12 Hyphophore scales very broad (0.7–1.2 mm) and very short, closely adnate to the surface, forming dark brown, lunular structures at the thallus margin (Costa Rica and Argentina) *G. fantasticum*
- 12* Hyphophore scales much narrower, pale or brownish black in a single species (*G. atosquamulatum*) 13
- 13 Hyphophore scales brownish black to pure black, narrowly flabelliform to triangular, projecting horizontally from the thallus margin (Kenya) *G. atosquamulatum*
- 13* Hyphophore scales paler (at most orange to pale brown or greyish), whitish to translucent or absent but diahyphal mass sometimes dark greyish brown 14
- 14 Thallus greenish to greenish grey, finely verrucose, mostly with a cellular cortex; hyphophores laminal and with vertically to obliquely orientated scales 15
- 14* Thallus silvery grey or shiny grey, areolate-bullate, or areolate (=with thin greenish marginal parts lacking crystals), mostly with a cartilaginous cortex; hyphophores mostly marginal and with horizontally oriented scales 19
- 15 Hyphophore scales triangular, their base immersed into a semicircular, crystalline bulge 16
- 15* Hyphophore scales blunt or with two lateral projections, crystalline bulge absent 17
- 16 Thallus verrucae typically arranged into radiate ridges (Australasia) *G. radiatum*
- 16* Thallus verrucae not arranged into radiate ridges (Australasia) *G. verruculosum*
- 17 Apothecia, especially when young, covered with a thin layer containing a brown pigment; mature apothecia with a greenish to yellowish brown disc and a reddish brown margin (Tropical Africa and Papua New Guinea) *G. fuscum*
- 17* Apothecia not covered with a brownish layer; mature apothecia with a yellowish green disc and a whitish margin 18
- 18 Hyphophore scales narrowly squamiform, blunt or with an irregular margin (west Caucasus and Macaronesia) *G. colchicum*
- 18* Hyphophore scales broadly squamiform, with two acute, lateral projections (Pantropical) *G. filicinum*
- 19 Thallus areolate: crystals clearly limited to certain parts of the thallus which appear as flat, silvery grey areoles surrounded by thin, greenish parts lacking crystals 20
- 19* Thallus areolate-bullate: crystals compact, completely invading the whole thallus (inner parts thinner and slightly verrucose in *G. gahavisukanum*) 22
- 20 Hyphophores marginal, their scales horizontally orientated and with a coarsely dentate margin, originating at the margin of enlarged parts of the thallus that are connected to its main part via narrow lobes (Cuba) *G. palmicola*
- 20* Hyphophores submarginal, their scales obliquely to vertically orientated and with two lateral projections or distorted and irregularly incised to lacinate 21
- 21 Hyphophore scales well developed, straight and usually with two lateral projections, pale orange to greyish (Tropical America) *G. areolatum*
- 21* Hyphophore scales usually distorted and irregularly incised to lacinate, sometimes reduced to clusters of membranaceous lobes, pale greyish or whitish, sometimes with a bluish tinge at their base (Pyrenees and southern Italy) *G. puntilloi*
- 22 Hyphophores very rare, laminal to submarginal, their scales obliquely orientated, blunt to irregularly incised; apothecia usually abundant (Pantropical and extending into subtropical and warm-temperate areas) *G. caucasicum*
- 22* Hyphophores usually abundant, marginal, their scales horizontally orientated, rarely almost vertical (*G. ciliatum*), flabelliform to narrowly triangular or setiform; apothecia usually rare or absent (abundant in *G. ciliatum*) 23
- 23 Hyphophore scales setiform and almost vertically orientated, forming thin cilia at the thallus margin; apothecia abundant (Pantropical) *G. ciliatum*
- 23* Hyphophore scales flabelliform to narrowly triangular, horizontally orientated; apothecia rare or absent 24

continued

KEY TO THE SPECIES OF *Gyalectidium* – continued

- 24 Hyphophores obliquely orientated, their scales triangular when well-developed but usually lacinate, strongly bluish grey when young, usually becoming whitish and sometimes translucent when old (Canary Islands and southern Italy) *G. minus*
- 24* Hyphophores horizontally orientated, their scales usually entire 25
- 25 Hyphophores triangular to narrowly triangular or even almost setiform, with straight sides and acute apex 26
- 25* Hyphophores flabelliform to liguliform, with rather rounded sides and obtuse to slightly irregular margin 27
- 26 Hyphophores very narrowly triangular to almost setiform (0.07–0.15 mm long and at most 0.05 mm broad at the base) (Australasia) *G. novoguineense*
- 26* Hyphophores triangular (0.05–0.1 mm long and broad) (Neotropics) *G. maracae*
- 27 Hyphophores rather large (0.2–0.3 mm long and 0.1–0.2 mm broad) and flabelliform, when typical with their longer size at mid-height with entire to irregularly incised upper margin (Australasia) ..
..... *G. flabellatum*
- 27* Hyphophores smaller and liguliform 28
- 28 Hyphophores 0.15–0.25 mm long and 0.1–0.15 mm broad, with a strong bluish grey tinge at their base, basally inserted into crystalline bulges; inner parts of the thallus rather thin and slightly verrucose (Papua New Guinea) *G. gahavisukanum*
- 28* Hyphophores 0.1–0.2 mm long and 0.1 mm broad, without any bluish grey tinge, whitish translucent, not inserted into crystalline bulges; inner parts of the thallus not thin, nor verrucose (Australia) ...
..... *G. australe*

chacos District, Ol Doinyo Sapuk east of Thika, 1°03'S, 37°05'E, 2100 m, 1985, Kalb & Schrögl s.n. (KALB, holotypus).

Description. THALLUS forming rounded to irregular, single or dispersed patches 1–3 mm diam, finely verrucose, greenish to whitish grey. HYPHOPHORES marginal, their scales small, developing from a thin brownish layer at first covering the diahyphal mass, horizontally orientated, narrowly flabelliform to triangular, and with entire to very slightly irregular margins, 0.1–0.2 mm broad and long, brownish black to black. APOTHECIA rounded, 0.1–0.2 mm diam., with pale brown disc and darker brown margin. ASCOSPORES ellipsoid, 30–50 × 12–20 µm. PYCNIDIA not found.

Notes. *Gyalectidium atosquamulatum* is easily recognized by its small, brownish black to black hyphophore scales. The only other species with brownish black scales is *G. fantasticum*, but here the scales are extremely broad and very short, and provided with two short, lateral projections. *G. atosquamulatum* resembles and seems to be most closely related to *G. imperfectum*, which has similar thallus and apothecia but differs in the reduced or absent, translucent hyphophore scales, while the dark colour of the hyphophores is caused by the upper layer of the diahyphal mass.

Distribution and ecology. This new species is known only from the type locality in a montane rain forest in Kenya, where it was found with the new *G. kenyanum*.

Gyalectidium australe Lücking sp. nov.

(Fig. 31)

A *Gyalectidio caucasico* thallo disperso et hyphophoribus liguliformibus albidusque, in margine thallorum formatis differt. Typus: AUSTRALIA. Queensland: Curtain Fig Tree State Forest Park, 17°17'S, 145°34'E, 700 m, 1994, Streimann 54029A (CANB, holotypus; hb. Lücking, isotypus).

Description. THALLUS forming minutely dispersed, rounded patches 0.2–0.3 mm diam., together forming well-delimited aggregates 2–5 mm diam., areolate-bullate due to strong encrustation with a continuous layer of crystals, silvery to whitish grey. HYPHOPHORES marginal, their scales small, one or several emerging from each individual thallus patch, therefore often overlapping, horizontally orientated, liguliform, 0.1–0.2 mm long and 0.1 mm broad, whitish translucent. APOTHECIA angular-rounded, 0.2–0.3 mm diam., with pale yellowish brown to greyish, thinly pruinose disc and prominent, whitish margin. ASCOSPORES ellipsoid, 30–40 × 12–18 µm. PYCNIDIA not found.

Notes. *Gyalectidium australe* is closely related to *G. caucasicum* but differs by its smaller and more regular thallus at the margin of which small, liguliform and horizontal hyphophores are produced. It is also closely related to *G. gahavisukanum*, known from a single locality in Papua New Guinea, which has slightly larger hyphophores with a bluish grey tinge at their base and basally inserted into large submarginal crystalline bulges.

Distribution and ecology. The species is known only from Queensland in Australia, and can be considered as rare.

Additional specimen examined. AUSTRALIA. Queensland: Wrights Creek, Lake Eacham National Park, 17°16'S, 145°38'E, 680 m, 1994, Streimann 54014A (CANB, hb. Lücking).

Gyalectidium catenulatum (Cavalc. & A. A. Silva)
Ferraro, Lücking & Sérus.
(Fig. 18)

In Ferraro & Lücking, *Tropical Bryology*, 19: 64 (2000). Bas.: *Tauromyces catenulatus* Cavalc. & A. A. Silva in Cavalcante *et al.*, *Publ. Inst. Micol. Univ. Fed. Pern.* 647: 35 (1972). Typus: BRAZIL. Rondônia: Pôrto Velho, 1963, Xavier Filho 19321 (URM 35356, holotypus!).

Description. THALLUS forming rounded patches 2–5 mm diam., sometimes numerous and covering large areas of the leaf, smooth and lacking crystals, or rarely with a few, scattered ones, greenish grey to grey. HYPHOPHORES laminal, their scales well-developed, obliquely orientated, squamiform and usually with two acute lateral projections, often bent inwards or even cucullate, 0.3–0.5 mm long and 0.3–0.7 mm broad, whitish to pale greyish, or pale orange. APOTHECIA rounded but sometimes confluent, hardly raised over thallus level, 0.2–0.5 mm diam., sometimes confluent (clusters of 2–6 discs sometimes present), with greenish greyish disc and whitish to brownish grey margin, a faint, whitish pruina sometimes present on the disc and the margin. ASCOSPORES ellipsoid, 30–40 × 15–20 µm. PYCNIDIA not found.

Notes. *Gyalectidium catenulatum* is characterized by its smooth thallus lacking crystals, in combination with laminal hyphophores producing well-developed, often cucullate scales with lateral projections. A smooth thallus is otherwise known from *G. conchiferum* and *G. yahriae*. The hyphophores of the latter are of a very different type, while those of *G. conchiferum* are similar to *G. catenulatum* but marginal and with a rounded, entire margin lacking the two lateral projections.

The closest relative of *Gyalectidium catenulatum*

seems to be *G. filicinum*, which differs by the finely verrucose thallus and the smaller, more prominent apothecia. Both species were not separated previously, and *Tauromyces catenulatus* has been synonymized with *G. filicinum* by Lücking *et al.* (1998). The type of the former is, however, a very typical representative of the present taxon. The enrolled hyphophores seem to be a particular feature of this species; this character is however quite variable as some populations have almost straight hyphophores while in others the lateral sides even touch each other.

Distribution and ecology. Known throughout the Neotropics but not common. The species seems to be restricted to exposed situations such as the forest canopy.

Additional specimens examined. MEXICO. Unknown locality, 1980, Roskoski s.n. (LG). COSTA RICA. Limón: Braulio Carillo National Park, 10°12'N, 83°55'W, 400 m, 1991, Lücking 91-1002 (LG). Cahuita National Park, 9°44'N, 82°50'W, sea level, 1991, Lücking 91-2902 (Lücking, Lich. Fol. Exsic. 64, as *G. filicinum*, LG, hb. Lücking). Heredia: La Selva Biological Station, 10°26'N, 84°03'W, 50–100 m, 1997, Lücking 97-797, 97-799 (hb. Lücking); *ibid.*, 1997, Lücking 97-1253 (hb. Lücking). Cartago: Orosi Valley, 9°47'N, 83°51'W, 1200 m, 2000, Lücking 00-215 (hb. Lücking). Cañon, 35 km south-south-east of San José on Interamericana, 9°41'N, 83°55'W, 2500 m, 1991, Lücking s.n. (hb. Lücking). Tapantí National Wildlife Refuge, 9°46'N, 83°47'W, 1800 m, 1991, Lücking 91-3229 (hb. Lücking). GUADELOUPE. Basse-Terre: Rivière Rose, promenade de la chute Moreau, 260 m, 1996, Sérusiaux s.n. (LG). ECUADOR. Napo: Jatun Satcha Biological Station, 1°04'S, 77°35'W, 450 m, 1996, Lücking 96-143 (hb. Lücking). Yasuni Nature Reserve, Tiputini Biological Station, 0°36'S, 76°28'W, 300 m, 1999, Palice & Valencia s.n. (Vězda, Lich. Rar. Exs. 439, hb. Vězda, hb. Lücking). BRAZIL. Amazonas: Rio Preto, 3°10'S, 59°50'W, 40 m, 1993, Kalb & Kalb s.n. (hb. Kalb). São Paulo: Between Ubatuba and Paratí, 23°20'S, 45°00'W, sea level, 1979, Kalb & Plöbst s.n. (hb. Kalb). Rio Grande Do Sul: Yraí, Balneario Osvaldo Cruz, 1990, Cristóbal 2242, 2243 (CTES); *ibid.*, 1992, Krapovickas & Cristóbal 44125 (CTES). PARAGUAY. Misiones: west of Yacyretá Isl., 1988, Ferraro *et al.* 3682 (CTES). Canendiyú: 22 km of Colonia Nueva Esperanza, Itabó Private Reserve, 24°35'S, 54°48'W, 260 m, 1996, Schinini *et al.* 31571, 31575 (CTES). ARGENTINA. Corrientes: Depto. Ituzaingó, 41 km east of Ituzaingó, 1984, Tressens 3052 (CTES). Depto. Santo Tomé, Arroyo Chimiray, 1974, Krapovickas *et al.* 36751 (CTES). Misiones: Depto. General Belgrano, Colonia Andresito, Chacra 30, 1996, Vanni *et al.* s.n. (CTES). Depto. Guaraní, 1500 m, 1994, Maruňak 729, 733, 744, 777 (CTES). Predio Guaraní, 1995, Tressens *et al.* 5511,

5515 (CTES). Depto. Iguazú, Iguazú National Park, 1995, Maruñak 874 (CTES); *ibid.*, 1995, Vanni *et al.* 3526 (CTES); *ibid.*, 1995, Ferraro *et al.* 5054 (CTES), 5028 (hb. Lücking). Depto. Candelaria, Loreto, 1981, Ferraro 2404 (CTES). Río Negro: San Carlos de Bariloche, Puerto Blest, 1999, Ferraro 6310 (CTES, hb. Lücking).

Gyalectidium caucasicum (Elenk. & Woron.) Vězda
(Figs 26, 27)

Vězda, Folia Geobot. Phytotax., Praha, 18: 56 (1983). Bas.: *Sporopodium caucasicum* Elenk. & Woron., Jahrb. Pflanzenkrankh., St Petersburg, 2: 124 (1908). Syn.: *Calenia caucasica* (Elenk. & Woron.) Vězda, Sched. Lich. Sel. Exs., Fasc. LXI: 4, no. 1512 (1978). Typus: Georgia. 'Caucasus: Gagry, 1907, Bartelsen; or Suchum, Pacichirsk, 1904, Woronow' (LE?, not seen; for further details see Santesson, 1952: 356–357).

Description. THALLUS forming angular or rounded, single, dispersed or confluent patches 1–3 mm diam., sometimes much larger (up to 7 mm diam.), areolate-bullate due to strong encrustation with a continuous layer of crystals, silvery to whitish grey, sometimes with an 'icy' and minutely crystalline surface (especially in the western Caucasus). HYPHOPHORES rare or absent, laminal to submarginal, their scales well-developed, obliquely orientated, squamiform with irregular upper margins or rarely laciniate, 0.1–0.3 mm long broad, whitish to pale greyish. APOTHECIA usually present, angular-rounded, 0.2–0.3 mm diam., deeply immersed in the thallus, with pale yellowish brown to greyish, thinly pruinose disc and prominent, whitish margin. ASCOSPORES oblong-ellipsoid, 40–50 × 10–15 µm. PYCNIDIA not found.

Notes. *Gyalectidium caucasicum* is in the centre of a group characterized by areolate-bullate thalli with large, compact clusters or a continuous layer of crystals. Its hyphophores are very rare and to be found on the thallus surface near the margins, which distinguishes it from most other species placed in the *G. caucasicum* group, explained by continuous growth of the thallus after the production of the hyphophores and their eventual inclusion in the thallus. A similar phenomenon is sometimes seen in *G. gahavisukanum* and certain individuals of *G. minus*. The latter has been confused with *G. caucasicum* (see below).

We have made no attempt to locate and examine the type collection of this species and refer to Santesson (1952: 356–357) for further information on the matter. Indeed, the identity of the taxon dealt with by Elenkin & Woronichin in their original description seems to be clear as only two other species of *Gyalectidium* are known from the large collections now available from

the Western Caucasus (*G. colchicum* and *G. setiferum*), and these are easily distinguished from *G. caucasicum* (Vězda, 1983; Sérusiaux, 1993).

Gyalectidium caucasicum is often attacked by the hyphomycete *Hansfordiellopsis lichenicola* (Batista & Maia) Deighton.

Distribution and ecology. Obviously pantropical but rather rare; populations that lack hyphophores cannot be determined with certainty, and hence, the distribution of *Gyalectidium caucasicum* is uncertain. It seems to prefer more open and drier situations than *G. filicinum* and associates with *Bullatina aspidota* (Vain.) Vězda & Poelt and *Asterothyrium* species. It is of interest that the species is found in northern Iran and the western Caucasus but not in Europe, nor in Macaronesia.

Selected specimens examined. GUATEMALA. Alta Verapaz: Near Coban, 1260–1440 m, 1939, Standley 71556 (F, filed under *Asterothyrium rotuliforme*). NICARAGUA. Masaya: Sierra de Managua, Las Nubes, 650 m, 1947, Standley 8737 (F, filed under *Strigula smaragdula*). COSTA RICA. Cartago: Orosi valley, 83°51'N, 09°47'N, 1150 m, 1992, Lücking 92-2913 (hb. Lücking). Limón: Cahuita village, 1988, Lücking 88-270 (hb. Lücking). BRAZIL. Bahia: Chapada Diamantina, Serra do Tombator, between Mundo Novo and Morro de Chapeú, 11°50'S, 40°45'W, 800 m, 1980, Kalb & Marcelli s.n. (hb. Kalb). PARAGUAY. Caazapá: Distrito Yuty, 15 km south of Capitindy, 1987, Arbo 2937b (CTES). Guairá: Colonia Independencia, 25° 45'S, 56°13'W, 250 m, 1986, Schinini 25353 (CTES). Amambay: Cerro Corá, VIII. 1980, Schinini & Bordas 20774 (CTES); Cerro Corá National Park, 1988, Ferraro *et al.* 3419 (CTES). Alto Paraná: Limoy Biological Reserve, 24°45'S, 54°45'W, 1996, Schinini *et al.* 31536 (CTES). ARGENTINA. Corrientes: Depto. Capital, Riachuelo, 1996, Ferraro 5326 & 5328 (CTES). Depto. Sto. Tomé, Arroyo Chimiray, 1974, Krapovickas *et al.* 36752 p.p. (hb. Lücking). Formosa: Depto. Capital, Estancia Guaycolec, 1995, Ferraro *et al.* 4612, 4634 (CTES). Misiones: Depto. Guaraní, 1500 m, 1994, Maruñak 732, 794 (CTES), 746 (hb. Lücking). Predio Guaraní, 1994, Tressens 5509 (CTES). Depto. Iguazú, Iguazú National Park, 1995, Ferraro *et al.* 5097 (CTES); *ibid.*, 1995, Vanni *et al.* 3511 (CTES). Depto. General Belgrano, Colonia Andresito, Chacra 30, 1996, Vanni *et al.* 3657 (CTES). RUSSIA. Krasnodar: Chosta valley near Soci, 150 m, 1973, Pisút s.n. (Vězda, Lich. Sel. Exs. 1179, as *G. filicinum*, LG). GEORGIA. Colchis: Sukhumi, 30–50 m, 1977, Vasák & Vězda s.n. (Vězda, Lich. Sel. Exs. 1512, as *G. filicinum*, LG); *ibid.*, 250 m, 1977, Vasák & Vězda s.n. (Vězda, Lich. Sel. Exs. 1513, as *G. filicinum*, LG); *ibid.*, 200–300 m, 1983, Vasák s.n. (hb. Lücking). TANZANIA. Morogoro region: Nguru

Mts, 900–1250 m, 1987, Pócs 87227 (Vězda, Lich. Sel. Exs. 2156, 2431, LG, hb. Lücking). SOUTH AFRICA. Transvaal: Drakensberg Mt, Lone Creek west of Sabie, 1100 m, 1982, Lambinon & Sérusiaux 82/161 (LG). Cape Province: Knysna, 1975, Liebold s.n. (STU, hb. Lücking, filed under *G. ciliatum*). IRAN. Mázanderán: Sissengân Forest Park, east of Nau Shahr, 10 m, 1976, Lambinon 76/273 (LG). JAPAN. Higo: Kyushu, 1956, Togashi s.n. (TNS). PAPUA NEW GUINEA. Madang: Gogol river, 5°20'S, 145°43'E, 30 m, 1987, Lambinon 87/330 (LG). Brahman Mission, 5°54'S, 145°20'E, 100 m, 1995, Sérusiaux 15707 (LG). Eastern Highlands: Mt Gahavisuka Provincial Park, 2300–2450 m, 6°01'S, 145°25'E, 1992, Sérusiaux 13762-15 (LG). Simbu: Mt Wilhelm, 2800 m, 5°55'S, 145°09'E, 1992, Sérusiaux 14108-7 (LG). AUSTRALIA. New South Wales: Border Ranges, Pinnacle Hill, 28°25'S, 153°07'E, 910 m, 1998, Streimann 61238 (CANB). Queensland: Curtain Fig Tree State Forest Park, 17°17'S, 145°34'E, 700 m, 1994, Streimann 54029A (CANB). NEW CALEDONIA. Province Sud: Noumea, I. 1887, Savès 51-54 (G).

Gyalectidium ciliatum Lücking, G. Thor & T. Matsumoto
(Figs 36, 37)

In Thor *et al.*, Symb. Bot. Ups. 32(3): 42 (2000). Typus: JAPAN. Kyushu (Kagoshima, Oshumi): 14 km south-west of Anbo, 30°14'N, 130°31'E, 50 m, 1994, Thor 12454 (TNS, holotypus!; UPS, isotypus!).

Description. THALLUS forming angular-rounded patches 1–3 mm diam., areolate-bullate due to encrustation with a continuous layer of crystals, silvery grey, marginally sometimes with a thin, greenish thallus zone. HYPHOPHORES marginal, obliquely to vertically orientated, setiform and thus typically cilia-like, 0.1–0.2 mm long and 10–20 µm broad, whitish. APOTHECIA angular-rounded, 0.25–0.4 mm diam., with pale to dark yellowish brown, sometimes thinly pruinose disc, and prominent, whitish margin. ASCOSPORES ellipsoid-ovoid, 35–45 × 15–20 µm. PYCNIDIA not found.

Notes. *Gyalectidium ciliatum* represents the ultimate reduction of hyphophores in the *G. caucasicum* group: they are cilia-like and can hardly be recognized as hyphophores unless their base (where diahyphae are produced) is carefully examined, which is the reason why the species had been tentatively placed in *Calenia* before its formal description (Lücking, 1997).

Distribution and ecology. *Gyalectidium ciliatum* is a rare taxon, known from a few localities in Japan (Thor *et al.*, 2000) and Costa Rica (Lücking 1997, as *Calenia ciliata*), a single locality in South Africa, and another

one on the island of La Réunion in the Indian ocean.

Additional specimens examined. COSTA RICA. Cartago: Guayabo National Monument, 9°59'N, 83°43'W, 1000 m, 1992, Lücking 92-2125 (hb. Lücking). Heredia: La Selva Biological Station, 10°26'N, 84°03'W, 50 m, 1991, Lücking 91-5621 (hb. Lücking). Limón: Hitoy Cerere Biological Reserve, 9°41'N, 83°02'W, 100–200 m, 1991, Lücking 91-985 (hb. Lücking). Puntarenas: Wilson's Botanical Gardens near San Vito, 8°48'N, 82°57'W, 1000 m, 1991, Lücking 91-4164 (hb. Lücking). San José: Quebradas Private Reserve, 9°29'N, 83°42'W, 1000–1100 m, 1992, Lücking 92-4379 (hb. Lücking). SOUTH AFRICA. Cape Province: Knysna, 1975, Liebold s.n. (STU, hb. Lücking). LA RÉUNION. Forêt de Bebouv, 1996, G. B. Feige s.n. (LG). JAPAN. See Thor *et al.* (2000).

Gyalectidium colchicum Vězda
(Fig. 13)

Vězda, Folia Geobot. Phytotax., Praha, 18: 58 (1983). Typus: RUSSIA. Colchis: Lazarevskoje, Dagomys, 250 m, 1979, Vězda s.n. (herb. Vězda, holotypus!; Vězda, Lich. Sel. Exs. 1866, isotypi, LG!).

Description. THALLUS forming rounded, single or dispersed to confluent patches 0.5–1.5(–3.0) mm diam., finely verrucose, greenish to whitish grey. HYPHOPHORES laminal, their scales well-developed, obliquely to vertically orientated, narrowly squamiform and with the upper margin blunt to irregularly incised, sometimes bent inwards and even with lateral sides touching each other, 0.15–0.2 mm long and 0.1–0.15 mm broad, whitish to pale yellowish or greyish, rarely dark bluish. APOTHECIA rare (only found in collections from Madeira), rounded but sometimes laterally confluent, 0.2–0.3 mm diam., with pale green to brownish grey disc and pale grey to brownish, sometimes rather dark brown or dark bluish margin. ASCOSPORES ellipsoid, 30–40 × 13–18 µm. PYCNIDIA rare, forming dark bluish, slightly raised spots on the thallus surface. CONIDIA bacilliform to slightly bifusiform, 2–3 × 0.7 µm.

Notes. *Gyalectidium colchicum* is a typical representative of sect. *Gyalectidium* and is most closely related to *G. filicinum*, from which it is easily distinguished by the narrower, sometimes enrolled, hyphophore scales with blunt upper margin.

Distribution and ecology. The species is known from the western part of the Caucasus (Russia and Georgia; Vězda, 1983) and from Macaronesia (Azores: São Miguel and Terceira; Madeira; Canary Islands: Gomera and La Palma). In both parts of its range, the species is often attacked by the lichenicolous hyphomycete

Hansfordiellopsis lichenicola (Batista & Maia) Deighton which seems to be able to obliterate its growth.

Additional specimens examined. RUSSIA. Colchis: Adler: Psacho valley, Kamenka, 200 m, 1979, Vězda s.n. (Vězda, Lich. Sel. Exs. 1868, LG). Soci: Agua river, Dzeperidze, 100–150 m, 1979, Vězda s.n. (Vězda, Lich. Sel. Exs. 1867, LG). SPAIN. Canary Islands, Gomera: Garagonay National Park, 1000 m, 1994, Sérusiaux s.n. (LG). La Palma: Los Tilos, 800–850 m, 1997, Sérusiaux s.n. (LG). PORTUGAL. Azores, São Miguel: Pico da Barrosa near Lagoa do Fogo, 900 m, 1986, Aptroot 16311 (hb. Aptroot). Pass between Furnas and Provoação, 350 m, 1986, Aptroot 16312 (hb. Aptroot). Terceira: Ribeira des Lapas, along 650–750 m, 1997, Schumacker 97/06/23 (LG). Madeira: Between Poiso and Ribeiro Frio, 1200 m, 1952, Eén & Persson s.n. (S). Ribeiro Frio, between Funchal and Santana, 850 m, 1979, Arvidsson s.n. (GB). Riba do Seixal, south of Seixal, 300–400 m, 1992, Sérusiaux s.n. (LG). Casas des Queimadas, 850–900 m, 1992, Sérusiaux s.n. (LG). Chão do Louros, 800 m, 1992, Sérusiaux s.n. (LG).

***Gyalectidium conchiferum* Lücking & Wirth sp. nov.**
(Fig. 19)

A *Gyalectidio catenulato* hyphophoribus conchiformibus in margine thallorum formati differt. Typus: CHILE. Los Lagos: Choshuenco, Volcán El Mocho, 600–630 m, 1999, Wirth & Feuerer 33909 (STU, holotypus).

Description. THALLUS forming rounded, single or dispersed patches 1–5 mm diam., smooth and lacking crystals, greenish grey to green. HYPHOPHORES marginal, their scales well-developed, vertically orientated, squamiform, mussel-shaped, at their base bent inwards towards the thallus margin, margin entire and rounded, 0.2–0.4 mm long and 0.3–0.4 mm broad, whitish. APOTHECIA and PYCNIDIA not found.

Notes. *Gyalectidium conchiferum* has the same, smooth and lacking crystals, thallus as *G. catenulatum*. Both species differ in their hyphophores: those of *G. catenulatum* are laminal and feature two acute, lateral projections, while those of *G. conchiferum* are bent inwards already at their base to form mussel-shaped structures with rounded margins.

Distribution and ecology. The species is known only from the type locality in Chile.

***Gyalectidium denticulatum* Lücking sp. nov.**

(Fig. 34)

A *Gyalectidio caucasicum* hyphophoribus in thallo immersis cum squamulis in segmentis anguste triangularibus vel setiformis divisio differt. Typus: COSTA RICA. Cartago: Orosi valley, 30 km east-south-east of San José, 9°47'N, 83°51'W, 1200 m, 2000, Lücking 00-227 (CR, holotypus; isotypi to be distributed in Lücking, Lich. Fol. Exs.).

Description. THALLUS forming rounded patches 2–5 mm diam., areolate-bullate to marginally rugose due to strong encrustation with a continuous layer of crystals, silvery grey. HYPHOPHORES laminal and immersed into the thallus surface, formed by small, rounded depressions, 0.15–0.2 mm diam., their scales divided into narrowly triangular to setiform segments, arranged in a circle from the margin of the hyphophores, obliquely orientated and pointing towards the centre, 0.05–0.1 mm long and 10–15 µm broad, the scales whitish, the diahyphal mass green. APOTHECIA and PYCNIDIA not found.

Notes. *Gyalectidium denticulatum* is one of the most fascinating lichens found during this study as, without careful examination, it would have been recorded as the widespread and ubiquitous *G. caucasicum*. Indeed, its thallus is identical with that of the latter; its hyphophores look like postmature apothecia without hymenium and reveal their nature only on closer, microscopic examination. This highly derived hyphophore type is shared only with *G. kenyanum*, in which the scale segments are slightly but distinctly longer and larger. Moreover, the diahyphal mass is typically green in *G. denticulatum* while it is greyish in *G. kenyanum*.

Distribution and ecology. Known only from the rich type collection in Costa Rica, where it was found on the leaves of trees along a road, and thus in rather disturbed vegetation. The new *G. laciniatum* was found in the same collection.

***Gyalectidium eskucheii* Sérus.**

(Fig. 39)

In Sérusiaux & De Sloover, Veröff. Geobot. Inst. Zürich 91: 269 (1986). Typus: BRAZIL. Rio Grande do Sul: Foz do Iguazú, 1983, De Sloover s.n. (LG, holotypus!).

Description. THALLUS forming rounded to irregular patches 1–3 mm diam., finely verrucose to almost smooth, sometimes with a few, scattered and rather large areoles, greenish to greenish grey. HYPHOPHORES

laminal, their scales well-developed, obliquely to vertically orientated, divided into 5–7(–10) narrowly triangular, often bended or twisted lobes arranged in a circle around the diahyphal mass, 0.3–0.5 mm long, whitish translucent to pale greyish. APOTHECIA rare, found only in specimens with depauperate hyphophores [Argentina, Tressens 2562 (CTES)], rounded, 0.1–0.2 mm diam., with brownish disc and margin. ASCOSPORES not found. PYCNIDIA not found.

Notes. *Gyalectidium eskucheii* is immediately recognized by its hyphophores, with the scale divided into a circle of narrowly triangular lobes. It is similar to *G. setiferum*, but in the latter, the diahyphal mass is yellowish green, sessile and rather convex, and surrounded by the setae, while in *G. eskucheii*, the diahyphal mass is adnate to the thallus surface, forming a dark greyish brown spot from which the circle of setae emerges. In addition, *G. setiferum* features sterile setae not associated with hyphophores.

Gyalectidium eskucheii seems also to be related to *G. imperfectum*, which has the same apothecial type but is easily distinguished by its highly reduced or completely absent hyphophore scales. Indeed, in the original description of *G. eskucheii*, it was assumed that the hyphophores of *G. imperfectum* represent young stages of that species (Sérusiaux & De Sloover, 1986), while subsequently it became clear that two different taxa are involved. Furthermore, the apothecia assumed to be those of *G. eskucheii* by Sérusiaux & De Sloover (1986) actually belong to *G. imperfectum*.

Distribution and ecology. Common in southern South America and also found in the Natal province of South Africa. The best developed populations are to be found in northern Argentina and adjacent Paraguay where numerous, small, rounded patches with 1–2 hyphophores can cover entire young leaves. The species is more difficult to detect on older leaves on which a complex and diverse lichen flora has developed; in such situations, only isolated and scattered thalli can be found.

Selected specimens examined. BRAZIL. Rio Grande Do Sul: Yraí, Balneario Osvaldo Cruz, 1992, Krapovickas & Cristóbal 44108a (CTES). PARAGUAY. Amambay: Cerro Guazú, 1980, Schinini *et al.* 20723 (CTES, LG). West limit of Cerro Corá National Park, 1988, Ferraro *et al.* 3466a (CTES). ARGENTINA. Corrientes: Depto. Ituzaingó, Río Aguapey, 1980, Tressens 2562 (CTES). Depto. Santo Tomé, Arroyo Chimiray, 1974, Krapovickas *et al.* 36752 p.p. (CTES, LG, hb. Lücking); *ibid.*, 3 km south-west of Gobernador Virasoro, 1982, Tressens 2126 (CTES). Depto. San Cosme, Paso de la Patria, arroyo San Juan, 1985, Ferraro 3235 (CTES). Jujuy: Gral. San Martín, Calilegua National Park, 1998, Ferraro *et al.* 5899, 5901, 5906 (CTES). Misiones:

Depto. Guaraní, 1500 m, 1994, Maruñak 747, 777 (CTES, hb. Lücking). Predio Guaraní, 1995, Tressens *et al.* 5511 (CTES); *ibid.*, 1999, Ferraro *et al.* 6103 (CTES, hb. Lücking). Depto. Apostóles, 6 km south of San José, 1979, Arbo *et al.* 2388 (CTES). SOUTH AFRICA. Natal: Nkandla Forest, 1150 m, 1982, Lamblinon & Sérusiaux 82/265 & 82/266 (LG).

***Gyalectidium fantasticum* Ferraro & Lücking sp. nov.**

(Fig. 23)

A *Gyalectidio areolato* thallo minore et hyphophoribus latioribus, applanatis-adnatis, fusconigris differt. Typus: PARAGUAY. Canendiyú: 22 km of Colonia Nueva Esperanza, Itabó Private Reserve, 24°35'S, 54°48'W, 260 m, 1996, Schinini *et al.* 31568 (CTES, holotypus).

Description. THALLUS made or rounded or irregular patches 1–2 mm diam., areolate, with whitish, applanate, polygonal crystalline clusters in the thallus centre surrounded by thin greenish thallus parts, rarely almost smooth. HYPHOPHORES marginal, their scales well-developed, horizontally orientated and completely adnate to the thallus, very broadly squamiform to almost lunulate and usually with two short lateral projections, 0.1–0.2 mm long and 0.7–1.2 mm broad, dark greyish brown or almost black at the base and whitish translucent above. APOTHECIA and PYCNIDIA not found.

Notes. This new species differs from all others in the genus by its very broad, adnate hyphophores which are hardly raised over the thallus surface. The thallus structure and the marginal, horizontally orientated hyphophores indicate a relationship with *Gyalectidium areolatum* and its allies, but the hyphophores of the latter species are much narrower and usually pale. Externally similar hyphophores are known from *Hippocrepidea nigra* Sérus. (Aptroot *et al.*, 1997), a monotypic genus known from high elevations in Papua New Guinea, whose apothecia and diahyphae produced by the hyphophores are quite different from *Gyalectidium*.

Distribution and ecology. Known only from two distant localities in tropical America.

Additional specimens examined. COSTA RICA. Cartago: Tapantí National Wildlife Refuge, 9°46'N, 83°47'W, 1800 m, 1991, Lücking 91-3229a (hb. Lücking). PARAGUAY. Canendiyú: 22 km of Colonia Nueva Esperanza, Itabó Private Reserve, 24°35'S, 54°48'W, 260 m, X. 1996, 1996, Schinini *et al.* 31565, 31566 (both LG, topotypes), 31573, 31574 (both CTES, topotypes).

Gyalectidium filicinum Müll. Arg.

(Figs 10, 11)

Müller Argoviensis, Flora 64: 101 (1881). Syn.: *Ectolechia filicina* (Müll. Arg.) Vain., J. Bot. 34: 206 (1896); *Sporopodium filicinum* (Müll. Arg.) Zahlbr. in Engler & Prantl, Die natürlichen Pflanzenfamilien, Teil 1: 123 (1905). Typus: BRAZIL. Rio de Janeiro: Rio de Janeiro, s.d., Gardner 34 (G, lectotypus!).

Lecidea phyllocharis subsp. *glaucovirescens* Vain., Acta Soc. Faun. Fl. Fenn. 7: 29 (1890). Syn.: *Ectolechia glaucovirescens* (Vain.) Vain., Catalogue of Welwitsch's African Plants II: 428 (1901); *Sporopodium glaucovirescens* (Vain.) Zahlbr., Catal. Lich. Univ. 2: 679 (1924). Typus: BRAZIL. Rio de Janeiro: Rio de Janeiro, 1885, Vainio 184 (UPS, isotypus!).

Melittosporiopsis pseudopezizoides Rehm, Hedwigia 39: 91 (1900). Typus: BRAZIL. Rio de Janeiro: Rio de Janeiro, s.d., Ule 696b (S, lectotypus, not seen).

Melittosporiopsis pseudopezizoides f. *minor* Rehm, Hedwigia 39: 91 (1900). Syn.: *Melittosporiopsis minor* (Rehm) Sacc. & Syd. in Saccardo, Syll. 16: 751 (1902). Typus: BRAZIL. Rio de Janeiro: Tijuca, s.d., Ule 2402 (S, lectotypus, not seen).

Melittosporiopsis pseudopezizoides var. *psychotriae* Rehm, Hedwigia 44: 12 (1904). Typus: BRAZIL. Sta. Catharina: Blumenau, 1888, Ule 1114 (S, lectotypus, not seen).

Description. THALLUS forming rounded or irregular patches 1–5(–10) mm diam., finely verrucose, greenish to greenish grey. HYPHOPHORES laminal, their scales well-developed, obliquely orientated, broadly squamiform and typically with two acute, lateral projections, 0.3–0.4(–0.6 mm) long and 0.3–0.4 mm broad, pure white, or pale orange to whitish grey. APOTHECIA rounded, usually numerous and sometimes aggregate, 0.2–0.3(–0.4) mm diam., with a yellowish green disc and a whitish to pale greenish margin. ASCOSPORES ellipsoid, 30–40 × 13–18 µm. PYCNIDIA not found.

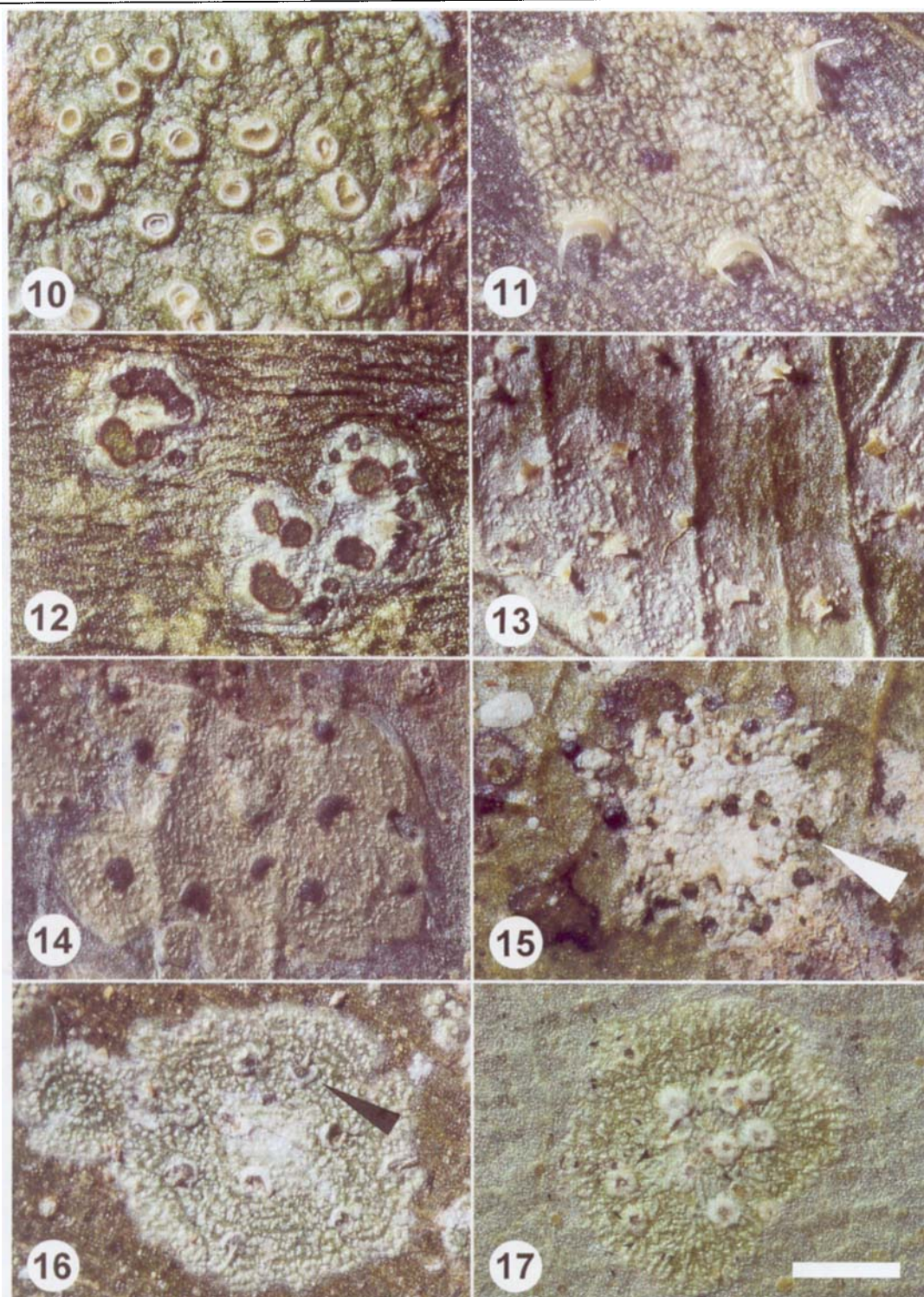
Notes. *Gyalectidium filicinum* is the most well-known representative of the genus. Basically the same thallus, apothecia and hyphophores are found in several other species which differ by radiate thallus ridges (*G. radiatum*), a brownish layer on the apothecia (*G. fuscum*), narrower and slightly different hyphophores partly immersed in basal crystalline bulges (*G. colchicum*, *G. verruculosum*), or a smooth thallus, sometimes with cucullate hyphophores (*G. catenulatum*). Contrary to most other species of the genus, *G. filicinum* always has a distinctly greenish apothecial disc, due to the abundance of epithelial algae which are sparse in other taxa.

Distribution and ecology. Pantropical, with a broad ecological amplitude. The species is found from lowland

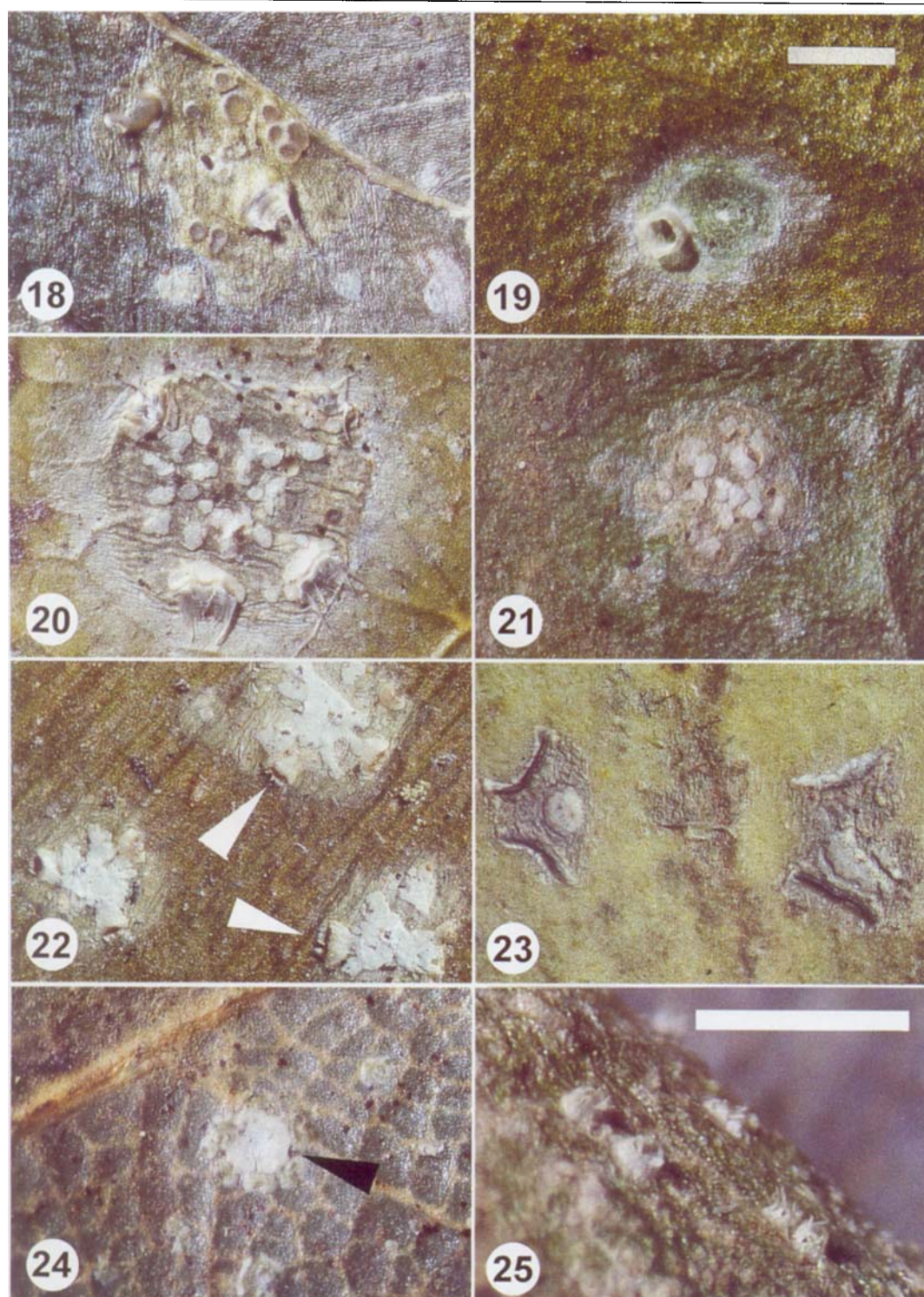
to upper montane rain forest, in quite different light regimes, from the shady understorey to the forest canopy, and also extends deeply into anthropogenic vegetation. It is most commonly found and best developed in natural light gaps within the forest. Hyphophores seem to be more frequently formed in open situations.

Gyalectidium filicinum has once been found on rocks at stream level in Guadeloupe (West Indies; Sérusiaux, 1998), an ecological niche rarely sampled by lichenologists in tropical areas and in which several lichens that are usually considered as genuine foliicolous are found. Indeed, in Guadeloupe, from the very same niche, *Echinoplaca verrucifera* Lücking and *Tricharia albostrigosa* R. Sant. were also collected.

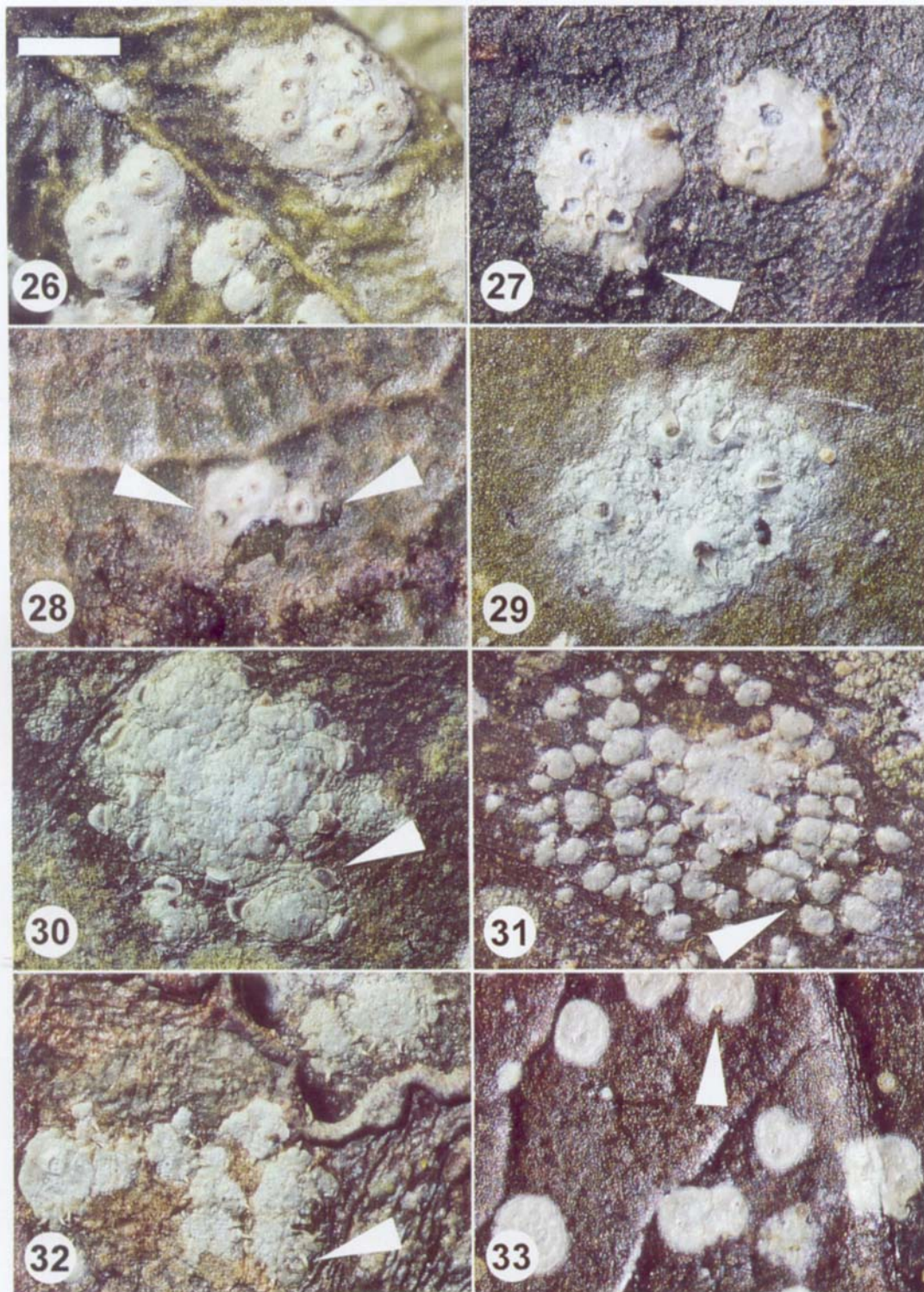
Selected specimens examined. COSTA RICA. Cartago: Guayabo national monument, 9°59'N, 83°43'W, 850–900 m, 1992, Lücking 92-1794 (Lücking, Lich. Fol. Exs. 13, LG). Orosi Valley, 9°47'N, 83°51'W, 1200 m, 2000, Lücking 00-370 (hb. Lücking). Limón: Cahuita National Park, 9°44'N, 82°50'W, sea level, 1991, Lücking 91-2902 (Lücking, Lich. Fol. Exs. 64). Puntaneras: Monteverde Biological Reserve, 10°16'N, 84°46'W, 1600–1700 m, 2000, Lücking 00-436 (hb. Lücking). Cocos Island National Park, 5°32'N, 87°04'W, 0–50 m, 1992, Lücking (Lücking, Lich. Fol. Exsic. 139, LG). NICARAGUA. Masaya: Sierra de Managua, Las Nubes, 650 m, 1947, Standley 8737 (F, filed under *Strigula smaragdula*). GUADELOUPE. Basse-Terre, Cascades aux Ecrevisses, Grande Traversée, 180 m, 1995, Sérusiaux s.n. (LG); ibid., Rose river, 260 m, 1996, Sérusiaux s.n. (LG). ST. LUCIA. Quillesse Forest Reserve, 300–350 m, 1993, Sérusiaux s.n. (LG). GUYANA. Demerara/Mahaica: Timehri, 6°35'N, 58°12'W, sea level, 1996, Lücking 96-3091 (BRG). ECUADOR. Pichincha: Guajalito Biological Station, 0°09'S, 78°39'W, 1800 m, 1996, Lücking 96-199 (QCA), 96-1094 (QCNE). BRAZIL. Amazonas: Rio Preto, 3°10'S, 59°50'W, 40 m, 1993, Kalb & Kalb s.n. (hb. Kalb). São Paulo: between Ubatuba and Parati, 23°20'S, 45°00'W, sea level, 1979, Kalb & Plöbst s.n. (hb. Kalb). Rio Grande Do Sul: Irai, balneario Osvaldo Cruz, 1992, Krapovickas & Cristóbal 44106b (CTES). Santa Catharina: Piratuba, Cascata do Monje, 1992, Krapovickas & Cristóbal 44101a (CTES). BOLIVIA. La Paz: Coroico, 1996, Krapovickas 46792 (CTES, hb. Lücking). PARAGUAY. Guairá: Colonia Independencia, 25°45'S, 56°13'W, 250 m, 1986, Schinini 25313 (CTES). Itapúa: Isla Yacyretá, 56°41'W, 27°24'S, 1988, Ferraro 3669 (CTES). Caazapá: Distrito Yuty, 4 km south of Capitindy, 1987, Arbo 2904 (CTES). Misiones: W of Yacyretá Isl., 1988, Ferraro 3647 (CTES). Amambay: Cerro Corá, 1980, Schinini & Bordas 20807 (CTES). ARGENTINA. Formosa: Depto. Capital, Estancia Guaycolec, 22 km north of Formosa, 1995, Ferraro *et*



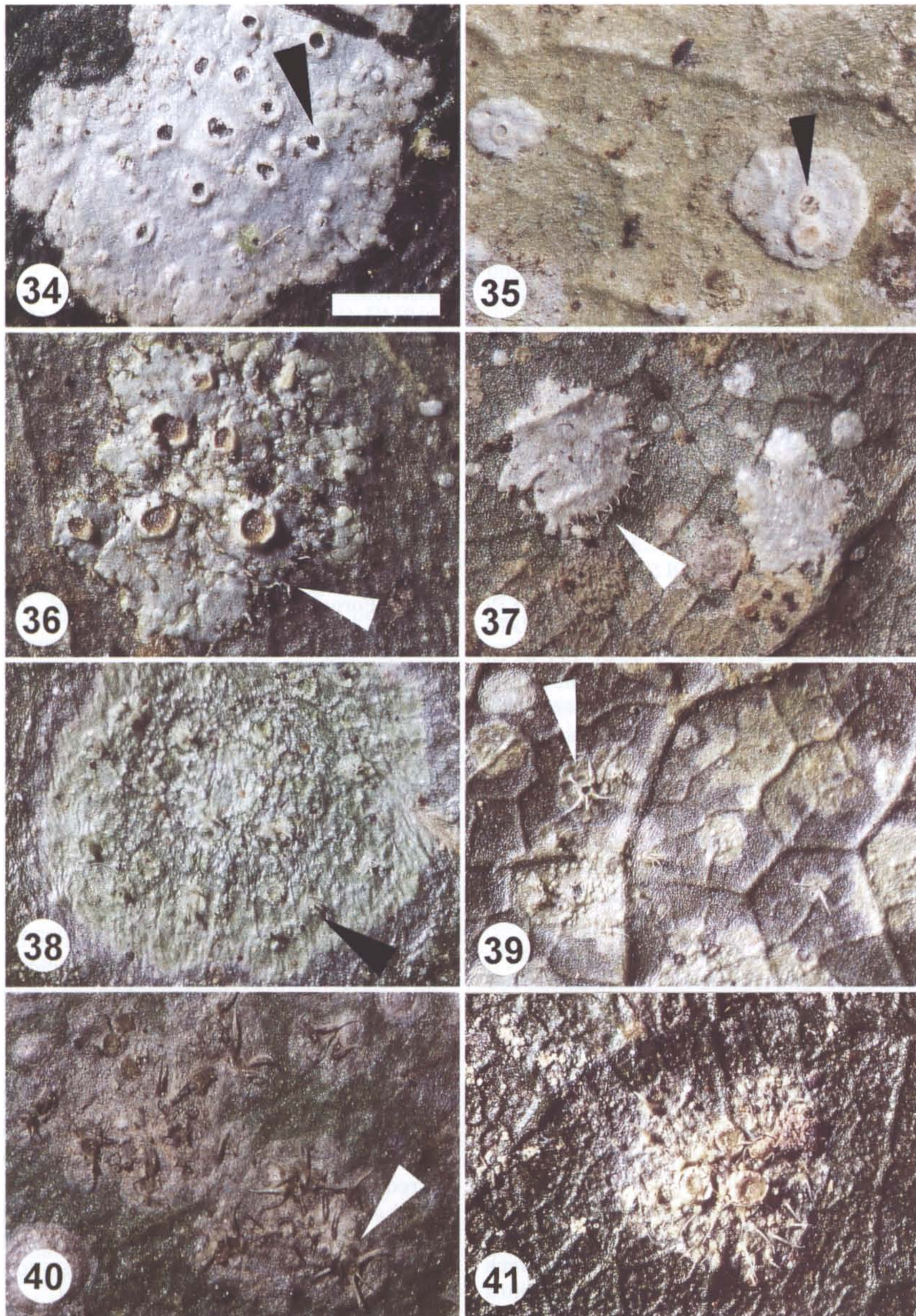
Figures 10–17. Species of *Gyalectidium* sect. *Gyalectidium*. Fig. 10. *G. filicinum* (Costa Rica, Lücking 96-672), thallus with apothecia. Fig. 11. *G. filicinum* (Costa Rica, Lücking 92-4764), thallus with hyphophores; note the acute lateral projections. Fig. 12. *G. fuscum* (an isotype), thallus with heavily pigmented apothecia. Fig. 13. *G. colchicum* (holotype), thallus with hyphophores. Fig. 14. *G. imperfectum* (Paraguay, Arbo *et al.* 2937a), thallus with hyphophores. Fig. 15. *G. atosquamulatum* (an isotype), thallus with hyphophores (arrow). Fig. 16. *G. verruculosum* (Australia, Streimann 54029a), thallus with hyphophores (arrow); note the crystalline bulges. *G. radiatum* (holotypus), thallus with apothecia; note the radiate ridges. Scale bar = 10 mm.



Figures 18–25. Species of *Gyalectidium* sect. *Areolectidium*. Fig. 18. *G. catenulatum* (Argentina, Maruñak 823), thallus with apothecia and two hyphophores. Fig. 19. *G. conchiferum* (an isotype), thallus with hyphophore. Fig. 20. *G. areolatum* (Argentina, Maruñak 735), thallus with hyphophores. Fig. 21. *G. puntilloi* (an isotype), thallus with crystalline areoles. Fig. 22. *G. palmicola* (holotype), thalli with hyphophores (arrows); note the apically dentate scales. Fig. 23. *G. fantasticum* (Paraguay, Schinini *et al.* 31573), thalli with hyphophores. Fig. 24. *G. membranaceum* (holotype), thallus with detached hyphophore (arrow). Species of *Gyalectidium* sect. *Gonioclectidium*. Fig. 25. *G. yahrae* (USA/Florida, Yahr 1025), thallus with hyphophores. Scale bar = 10 mm (same for 18–24).



Figures 26–33. Species of *Gyalectidium* sect. *Placolectidium*. Fig. 26. *G. caucasicum* (Vězda: Lich. Sel. Exs. 1512), thallus with apothecia. Fig. 27. *G. caucasicum* (South Africa, Liebold s.n.), thallus with apothecia and hyphophores (arrow). Fig. 28. *G. minus* (an isotype), thallus with apothecium and hyphophores (arrows). Fig. 29. *G. gahavisukanum* (an isotype), thallus with hyphophores; note the crystalline bulges. Fig. 30. *G. flabellatum* (holotype), thallus with hyphophores (arrow). Fig. 31. *G. australe* (an isotype), dispersed thallus with hyphophores (arrow). Fig. 32. *G. novoguineense* (Papua New Guinea, Demoulin 5889), thallus with hyphophores (arrow). Fig. 33. *G. maracae* (holotype), thalli with hyphophores (arrow). Scale bar = 10 mm.



Figures 34–41. Species of *Gyalectidium* with dissected hyphophores or setae (different sections). Fig. 34. *G. denticulatum* (an isotype), thallus with crateriform, minutely dentate hyphophores (arrow). Fig. 35. *G. kenyanum* (holotype), thallus with apothecium and crateriform, setose hyphophore (arrow). Fig. 36. *G. ciliatum* (an isotype), thallus with apothecia and ciliate marginal hyphophores (arrow). Fig. 37. *G. ciliatum* (Costa Rica, Lücking 92-4379), thallus with marginal ciliate hyphophores (arrow). Fig. 38. *G. laciniatum* (an isotype), thallus with lacinate hyphophores (arrows). Fig. 39. *G. eskucheii* (Argentina, Ferraro *et al.* 6121), thalli with ciliate hyphophores (arrow). Fig. 40. *G. setiferum* (holotype), thallus with setiform hyphophores surrounding a central, slightly prominent diahyphal mass (arrow). Fig. 41. *G. microcarpum* (South Africa, Vobis 508b), thallus with sterile setae. Scale bar = 10 mm.

al. 4625 (CTES). Chaco: Depto. San Fernando, Colonia Benitez, INTA reserve, 1979, Ferraro *et al.* 1789 (CTES); *ibid.*, 1980, Ferraro 2980 (CTES). Corrientes: Depto. Capital, Riachuelo, 1981, Ferraro 2214 (CTES). Depto. San Cosme, Paso de La Patria, 1993, Ferraro *et al.* 4565 (CTES). Depto. Saladas, 1985, Schinini 24359 (CTES). Depto. Santo Tomé, 35 km south-west of Santo Tomé, 1979, Ferraro *et al.* 1590 (CTES). Garruchos, Ea. San Juan Bautista, 1974, Krapovickas *et al.* 36724 (CTES). Depto. Ituzaingó, Rincón Ombú Chico, 1978, Schinini *et al.* 20113 (CTES). Misiones: Depto. Iguazú, Apepú Reserve, 1982, Ferraro *et al.* 2508 (CTES). Cataratas del Iguazú, 1982, Ferraro *et al.* 2595a (CTES). Iguazú National Park, 1995, Ferraro *et al.* 4985 (CTES). Depto. Guaraní, 1500 m, 1994, Maruñak *et al.* 727 (CTES). DEMOCRATIC REPUBLIC OF CONGO. Kivu: west side of Kahuzi, 58 km along the road Bukavu-Walikale, 1850 m, 1978, Lambinon 78/319 (LG). JAPAN. See Thor, Lücking & Matsumoto (2000). PAPUA NEW GUINEA. Madang: Mt Baiteta, 55 m, 1989, De Sloover 89L26 (LG). Eastern Highlands: Mt Gahavisuka Provincial Park, 6°01'S, 145°25'E, 2300–2450 m, 1992, Sérusiaux 13762-5 (LG). Central: Varirata National Park, 9°26'S, 147°21'E, 800 m, 1995, Sérusiaux 15485 (LG). Simbu: Mt Wilhelm, 5°47'S, 145°03'E, 3600 m, 1992, Sérusiaux 14023-4 (LG). AUSTRALIA. New South Wales: Border Ranges, Pinnacle Hill, 28°25'S, 153°07'E, 910 m, 1998, Streimann 61238 (CANB). NEW CALEDONIA. Nord: Koné, Mont Tanji, 700 m, 1976, MacKee 31695c (PC). Sud: Noumea, 1887, Savès 93 (G). Monts Koghis-Dumbéa, 22°14'S, 166°30'E, 550 m, 1994, Kalb & Kalb s.n. (hb. Kalb).

***Gyalectidium flabellatum* Sérus. sp. nov.**

(Figs 1–6, 30)

A *Gyalectidio caucasicum* hyphophoribus flabelliformibus, in margine thallorum formatis differt. Typus: PAPUA NEW GUINEA. Madang: Brahman Mission, south side of Ramu river, 5°54'S, 145°20'E, 100 m, 1995, Sérusiaux 15700 (LG, holotypus).

Description. THALLUS forming angular-rounded to almost lobulate-crenate patches 1–3 mm diam., areolate-bullate due to strong encrustation with a continuous layer of crystals, silvery to whitish grey but sometimes with thin greenish thallus parts at the margin. HYPHOPHORES submarginal to marginal, their scales well-developed but rather difficult to see, emerging from a low bulge, horizontally orientated, broadly flabelliform and with a slightly dentate upper margin, typically with its broadest size at mid-height, 0.1–0.2 mm long and 0.2–0.3 mm broad, whitish translucent to bluish grey. APOTHECIA angular-rounded, 0.2–0.3 mm diam., with pale yellowish brown to greyish, thinly pruinose

disc and prominent, whitish margin. ASCOSPORES ellipsoid, 30–45 × 10–17 µm. PYCNIDIA not found.

Notes. *Gyalectidium flabellatum* is distinguished by the typical shape of its hyphophores: when well developed, they are flabelliform and most typically with their broader size at mid-height. Most closely related is *G. australe*, which usually has a minutely dispersed thallus and narrower hyphophores.

Distribution and ecology. Known only from two localities: one along the northern coast of Papua New Guinea, where it occurs together with *Gyalectidium caucasicum* and *G. verruculosum*, and one in Queensland in Australia, associated with *G. australe* and *G. verruculosum*.

Additional specimens examined. PAPUA NEW GUINEA. Madang: Brahman Mission, 5°54'S, 145°20'E, 100 m, 1995, Sérusiaux 15806 (LG, topotypus). AUSTRALIA. Queensland: Curtain Fig Tree State Forest Park, 17°17'S, 145°34'E, 700 m, 1994, Streimann 54029A (CANB).

***Gyalectidium fuscum* Lücking & Sérus. sp. nov.**

(Fig. 12)

A *Gyalectidio filicino* apotheciis juvenilibus strato fusco obtectis differt. Typus: PAPUA NEW GUINEA. Eastern Highlands: Mt Gahavisuka Provincial Park, 6°01'S, 145°25'E, 2300 m, 1995, Sérusiaux 16203 (LG, holotypus; hb. Lücking, isotypus).

Description. THALLUS forming rounded, single or clustered patches 1–2 mm diam., finely verrucose, greenish to greyish. HYPHOPHORES rare, laminal, their scales well-developed, obliquely orientated, squamiform and typically with two acute, lateral projections, 0.3–0.5 mm long and 0.2–0.4 mm broad, whitish to pale greenish grey. APOTHECIA rounded, 1–4(–10) per thallus patch, 0.2–0.3 mm diam., with the disc at first covered by a thin, brown layer which is reduced to a narrow reddish brown zone in mature apothecia, margin distinctly raised, brown, sometimes with small, whitish verrucae which correspond to crystals accumulation underneath. ASCOSPORES ellipsoid, 35–45 × 14–20 µm. PYCNIDIA not found.

Notes. *Gyalectidium fuscum* is most closely related to *G. filicinum* from which it differs by the brownish to reddish brown apothecial margin. The brownish layer is typically covering the whole surface of young apothecia and is not caused by necrotic effects as demonstrated by apothecial sections. Similar brownish apothecia are otherwise known from *G. imperfectum* which differs by its completely different hyphophores.

Distribution and ecology. The species is known from the mountains of Papua New Guinea (incl. the type collection which is well-developed and exuberant), and several localities in tropical Africa.

Additional specimens examined. DEMOCRATIC REPUBLIC OF CONGO. Shaba: Plateau des Muhila, V. 1972, Malaisse 2047e (LG). Kivu: INRS Reserve, Luhoho river, 850 m, 1978, Lambinon 78/263 (LG). BURUNDI. Bubanza: Mugomero (Rugazi), 29°31'E, 03°13'S, 2200 m, 1981, Reekmans 10634 (LG). PAPUA NEW GUINEA. Simbu: Mt Wilhelm, Bundi Gap, 145°09'E, 5°48'S, 2800 m, 1992, Sérusiaux 13856-16 (LG).

Gyalectidium gahavisukanum Sérus. sp. nov.

(Fig. 29)

A *Gyalectidio caucasico* hyphophoribus liguliformibus cum obtusa apice et basi caesio-cinerea vel brunnea, in margine areolatum formati differt. Typus: PAPUA NEW GUINEA. Eastern Highlands: Mt Gahavisuka Provincial Park, 6°01'S, 145°25'E, 2300 m, 1995, Sérusiaux 16209 (LG, holotypus).

Description. THALLUS forming rounded patches 1–2 mm diam., areolate-bullate due to strong encrustation with a continuous layer of crystals but inner parts of the thallus comparatively thin and slightly verrucose, whitish grey to almost white on the areoles, greenish grey in inner parts. HYPHOPHORES submarginal to marginal, their scales well-developed, emerging outwards from a large, semicircular crystalline bulge, horizontally orientated, liguliform with obtuse upper margin, 0.15–0.25 mm long and 0.1–0.15 mm broad at the base, pale greyish to translucent except for the base which is bluish grey or brownish. APOTHECIA and PYCNIDIA not found.

Notes. *Gyalectidium gahavisukanum* belong to sect. *Placolectidium* and comes near *G. australe*, known from Australia, from which it is easily distinguished by its large submarginal crystalline bulges from which very regular, horizontally orientated, liguliform hyphophore scales emerge. These are slightly larger than those of *G. australe* and have a bluish grey tinge at their base.

Distribution and ecology. *Gyalectidium gahavisukanum* is known from a single locality in the mountains of Papua New Guinea (the Gahavisuka park after which the species is named).

Gyalectidium imperfectum Vězda

(Fig. 14)

Vězda, Nova Hedwigia 58: 131 (1994). Typus: AUSTRALIA. Queensland: Yungaburra road, 2 km south-east of Atherton, 17°16'S, 145°29'E, 850 m, 1983, Streimann s.n. (CBG 8302429, holotypus!).

Description. THALLUS forming rounded or irregular patches 3–6 mm diam., finely verrucose, greenish to whitish grey. HYPHOPHORES submarginal to marginal, their scales strongly reduced or absent, when present obliquely orientated, lacinate, 0.05–0.1 mm long and broad, translucent and membranaceous; the diahyphal mass visible as a reniform to lunular, dark greyish brown, 0.1–0.2 mm long and 0.2–0.4 mm broad spot. APOTHECIA rounded, 0.2–0.4 mm diam., rather flat, with a yellowish brown disc and a pale green to brownish margin. ASCOSPORES ellipsoid, 35–45 × 15–22 µm. PYCNIDIA not found.

Notes. *Gyalectidium imperfectum* is easily recognized by its adnate, dark brownish grey hyphophores lacking a distinct scale. When mature, they lose their rounded shape and become typically lunular; under more xeric ecological conditions, they sometimes develop a translucent, lacinate scale on their outer side. *G. membranaceum* also has adnate hyphophores reduced to horizontal spots, but here they are much thinner and membranaceous, and the thallus of that species is distinctly areolate instead of finely verrucose. The apothecia of *Gyalectidium imperfectum* are typically brownish and resemble those of *G. fuscum*.

Distribution and ecology. The species is pantropical but probably overlooked since it might have been mistaken for young *Gyalectidium filicinum*. Its ecology is rather similar but it seems to prefer slightly more open situations. Locally, populations with abundant hyphophores may cover entire leaves.

Selected specimens examined. USA. Florida: Apalachicola National Forest, 1976, Sérusiaux 1794 (Vězda, Lich. Sel. Exs. 1556, as *G. filicinum*, LG). Louisiana: Fricke's cave, south of Franklinton, 1976, Sérusiaux 1685 (LG). COSTA RICA. Cartago: Ujarras village, 9°49'N, 83°50'W, 1200 m, 1991, Lücking 91-2807 (hb. Lücking). Orosi Valley, 9°47'N, 83°51'W, 1200 m, 2000, Lücking 00-204, 00-368 (hb. Lücking). Limón: Braulio Carrillo National Park, 10°12'N, 83°05'W, 480 m, 1992, Lücking 92-5143 (hb. Lücking). Alajuela: Caño Negro, 10°54'N, 84°47'W, sea level, 1992, Lücking 92-2935 (hb. Lücking). Heredia: La Selva Biological Station, 10°26'N, 84°03'W, 50–100 m, 1999, Lücking 99-135 (hb. Lücking). Puntarenas: Monteverde Biological Reserve, 10°16'N, 84°46'W, 1600–1700 m, 2000, Lücking 00-417

(hb. Lücking). GUADELOUPE. Basse-Terre: north-east of La Madeleine, near 'Grand Etang', 400 m, 1995, Sérusiaux s.n. (LG). ST. LUCIA. Quillesse Forest Reserve, 300–350 m, 1993, Sérusiaux s.n. (LG). GUYANA. Demerara/Mahaica: Timehri, 6°35'N, 58°12'W, sea level, 1996, Lücking 96-3001 (BRG). ECUADOR. Pastaza: Mera, 4 km north of the village, 1100 m, montane rain forest, 1983, Arvidsson & Arvidsson 3916 (GB). Napo: Jatun Satcha Biological Station, 1°04'S, 77°35'W, 450 m, 1996, Lücking 96-144, 96-450 (hb. Lücking). Pichincha: Guajalito Biological Station, 0°09'S, 78°39'W, 1800 m, 1996, Lücking 96-211 (QCA), 96-1092 (QCNE). BRAZIL. Bahia: Porto Seguro, 16°25'S, 39°07'W, sea level, 1980, Kalb & Marcelli s.n. (hb. Kalb). PARAGUAY. Caazapá: Distrito Yuty, 15 km south of Capitindý, 1987, Arbo *et al.* 2937a (CTES). ARGENTINA. Corrientes: Depto. Ituzaingó, Río Aguapey, 1980, Tressens 2562 (CTES). Depto. Capital, 6 km south-west of Colonia Garabí, 1982, Tressens *et al.* 2135 (CTES); *ibid.*, Riachuelo, 1996, Ferraro 5317, 5320 (CTES). Depto. San Cosme, Paso de La Patria, 1985, Ferraro & Nash 3223 (hb. Lücking). Misiones: Depto. Guaraní, 1500 m, 1994, Maruñak 747, 777 (CTES). Predio Guaraní, 1995, Tressens *et al.* 5511 (CTES). Depto. Iguazú, Iguazú National Park, Ferraro *et al.* 5028 (hb. Lücking). DEMOCRATIC REPUBLIC OF CONGO. Kivu: west of Kahuzi, 58 km along the road Bukavu-Walikale, 1850 m, 1978, Lambinon 78/269 (LG). AUSTRALIA. New South Wales: Border Ranges National Park, 28°23'S, 153°04'E, 700 m, 1998, Streimann 61037B (CANB). Queensland: Curtain Fig Tree State Forest Park, 17°17'S, 145°34'E, 700 m, 1994, Streimann 54029A (CANB). NEW CALEDONIA. Nord: Koné, Mont Tanji, 700 m, 1976, MacKee 31695 (PC, hb. Lücking).

***Gyalectidium kenyanum* Lücking & Kalb sp. nov.**

(Fig. 35)

A *Gyalectidio denticulato* thallis minoribus hyphophoribus setiformibus majoribus differt. Typus: KENYA. Eastern: Machacos District, Ol Doinyo Sapuk east of Thika, 1°03'S, 37°05'E, 2100 m, 1985, Kalb & Schrögl s.n. (KALB, holotypus; hb. Lücking, isotypus).

Description. THALLUS forming rounded patches 1–3 mm diam., areolate-bullate due to strong encrustation with a continuous layer of crystals, silvery to whitish grey. HYPHOPHORES laminal and immersed into the thallus surface, usually 1–3 per thallus patch, formed by small, rounded depressions, 0.15–0.2 mm diam., their scales divided into narrowly triangular to setiform segments, arranged in a circle from the margin of the hyphophores, obliquely orientated and pointing towards the centre, 0.1–0.2 mm long and 10–20 µm broad, the scales whitish, the diahyphal mass greyish. APOTHECIA

angular-rounded, 0.15–0.25 mm diam., with pale yellowish brown to greyish, thinly pruinose disc and whitish margin. ASCOSPORES oblong-ellipsoid, 30–50 × 10–15 µm. PYCNIDIA not found.

Notes. This species is closely related to *Gyalectidium denticulatum* with which it shares the same hyphophore type. In *G. kenyanum*, however, the hyphophore scale segments are longer and usually cover the diahyphal mass which is greyish instead of green. In addition, the hyphophores are less numerous per thallus patch, and the thallus is smaller and lacks the marginally rugose structure typical of *G. denticulatum*.

Distribution and ecology. Known only from the type locality in a montane rain forest in Kenya, where it was found with the new *G. atrosquamulatum*.

***Gyalectidium laciniatum* Lücking sp. nov.**

(Fig. 38)

A *Gyalectidio filicino* hyphophoribus laciniatis in parte basali e verruca crystallina lunata emergentibus differt. Typus: COSTA RICA. Cartago: Orosi valley, 9°47'N, 83°51'W, 1200 m, 2000, Lücking 00-212 (CR, holotypus).

Description. THALLUS forming rounded patches 2–5 mm diam., finely verrucose, greenish to greenish grey. HYPHOPHORES laminal, their scales well-developed, usually emerging from a crescent-shaped, whitish, crystalline bulge, obliquely orientated, lacinate or with irregular lateral projections, 0.15–0.25 mm long and 0.2–0.3 mm broad, whitish translucent, sometimes slightly orange, the surface of the diahyphal mass greenish. APOTHECIA and PYCNIDIA unknown.

Notes. This new species is intermediate between *Gyalectidium verruculosum* and *G. eskucheii*. The hyphophore scales of the former are typically triangular but also emerge from a basal, crescent-shaped crystalline bulge. The scales of *G. eskucheii* are completely divided and thus look like setae and are arranged in a circle around the diahyphal mass which is dark brownish grey.

Distribution and ecology. Known only from the type collection in Costa Rica, where it was found on the leaves of trees along a road, and thus in rather disturbed vegetation. The new *G. denticulatum* was found in the same collection.

***Gyalectidium maracae* Lücking sp. nov.**

(Fig. 33)

A *Gyalectidio caucasicum* hyphophoribus cum squamulis minutissimis triangularibusque, in margine thallorum

formatis differt. Typus: COSTA RICA. Cartago: Orosi Valley, 9°47'N, 83°51'W, 1200 m, 2000, Lücking 00-211 (CR, holotypus).

= *Gyalectidium macaronesticum* Sérus. ined. in Lücking & Kalb (2000).

Description. THALLUS forming small, rounded, individual patches 1–2 mm diam., numerous patches usually covering the leaf surface, thinly areolate-bullate due to strong encrustation with an irregular to continuous layer of crystals, silvery to whitish grey. HYPHOPHORES marginal, their scales very small, horizontally arranged, triangular, 0.05–0.1 mm long and broad at the base, whitish translucent to pale grey. APOTHECIA rare, angular-rounded, 0.2–0.3 mm diam., with pale yellowish brown to greenish grey disc and slightly prominent, whitish margin. ASCOSPORES ellipsoid-ovoid, 35–50 × 15–20 µm. PYCNIDIA not found.

Notes. This species was at first believed to be identical with the European *G. minus* (known from southern Italy and the Canary Islands, and first named *macaronesticum* in preliminary draft) and was published under the name '*G. macaronesticum* Sérus. ined.' by Lücking & Kalb (2000). However, this species is different from *G. minus* and more closely related to *G. novoguineense*. To avoid any confusion, we have decided to dismiss the epithet *macaronesticum*, and to name this taxon after a musical instrument typical for South America (the maraca).

Gyalectidium maracae is indeed very similar to *G. novoguineense* but differs in the shorter and broader triangular hyphophore scales. It cannot be excluded that both taxa represent extremes of a single species, but thus far the differences between the Neotropical and Australasian material justify their separation.

Distribution and ecology. A very rare species, only known from the Neotropics.

Specimens examined. COSTA RICA. Cartago: Orosi Valley, 9°47'N, 83°51'W, 1200 m, 1992, Lücking 92-2913 (hb. Lücking, topotypus). BRAZIL. São Paulo: between Ubatuba and Paratí, 23°20'S, 45°00'W, sea level, 1979, Kalb & Plöbst s.n. (hb. Kalb).

***Gyalectidium membranaceum* Sérus. & Lücking**

sp. nov.

(Fig. 24)

A *Gyalectidio* speciebus hyphophoribus membranaceo caesio strato deminutis differt. Typus: SPAIN. Canary Islands, La Palma: Los Tilos, west of Las Lomados, south of Los Sauces, 800–850 m, 1997, Sérusiaux s.n. (LG, holotypus).

Description. THALLUS forming very small, rounded to crenate, ill-looking patches 0.05–0.1 mm diam., indistinctly areolate, with a whitish, appanate crystalline cluster in the centre surrounded by a thin greenish grey marginal zone. HYPHOPHORES marginal, their scales absent, hyphophores therefore reduced to a spot representing the diahyphal mass, covered by a thin, membranaceous layer, 0.07–0.1 mm diam., pale bluish grey; diahyphal mass often detached and thallus therefore appearing crenate. APOTHECIA and PYCNIDIA not found.

Notes. *Gyalectidium membranaceum* is characterized by its thin, meagre thallus with small hyphophores reduced to a membranaceous bluish layer covering the conidial mass. It closely resembles *G. imperfectum* which also has hyphophores reduced to adnate spots, but in the latter they are larger and more cartilaginous, and the thallus is finely verrucose. There is little doubt that the membranaceous layer together with the conidial mass (diahyphae and associated algal cells) form a genuine diaspore, as many thalli have a strongly crenate margin because of their removal as a whole, most probably by mechanical agents during dry periods. Dispersal of parts of the diahyphal mass can of course also take place with the water film running over the leaf surface, as it is expected to occur in all other species.

Distribution and ecology. Known only from the island of La Palma, the type locality being one of the best remnants of the evergreen subtropical cloud forest in the Canary Islands. *Gyalectidium membranaceum* is obviously very rare in its locality, as only a few leaves were found to host it. Quite interestingly, however, it was a pioneer species colonizing young leaves of Lauraceae together with *G. colchicum*.

***Gyalectidium microcarpum* (Vězda) Lücking, Sérus.**

& Vězda comb. nov.

(Fig. 41)

Bas.: *Calenia microcarpa* Vězda, Folia Geobot. Phytotax., Praha, 14: 55 (1979); *Bullatina microcarpa* (Vězda) Brusse, Mycotaxon 49: 11 (1993). Type: MALAYSIA. Solangor: Kuala Lumpur-Kuantan, Ulu Gombak Research Station, 80 m, 1974, D. J. Mabberley s.n. (hb Vězda, holotypus, not seen).

Description. THALLUS forming rounded patches 2–5 mm diam., coarsely but regularly verrucose, regularly furnished with whitish, up to 0.5 mm long sterile setae, greenish to whitish grey. HYPHOPHORES not found. APOTHECIA rounded, 0.15–0.25 mm diam., with pale yellowish brown disc and whitish margin. ASCOSPORES ellipsoid, 42–50 × 20–22 µm. PYCNIDIA not found.

Notes. This distinctive taxon is easily recognized by its coarsely verrucose thallus provided with numerous sterile setae. Although hyphophores have not been found, the phylogenetic analysis (Lücking *et al.*, in prep.) clearly indicates that this species is best included in *Gyalectidium*, as it has a typically small thallus and small, immersed apothecia in which the proper excipulum is separated from the thalline margin by a narrow slit.

Distribution and ecology. *Gyalectidium microcarpum* is a locally abundant species in the tropical and subtropical areas of Australasia, and has also been reported from Southern Africa. In subtropical areas of Australia, it forms characteristic communities together with *G. verruculosum* and *Sporopodium flavescens* (R. Sant.) Vězda.

Selected specimens examined. DEMOCRATIC REPUBLIC OF CONGO. Shaba: Plateau des Muhila, ravin de la rivière Lauila, 1982, F. Malaisse 2030e & 2042e (LG). SOUTH AFRICA. See Brusse (1993). PAPUA NEW GUINEA. Central: Musgrave River Road, 9°25'S, 147°27'E, 700 m, 1981, Streimann & Naoni 15928 (CANB). AUSTRALIA. New South Wales: Macquarie Pass National Park, 34°34'S, 150°41'E, 80 m, 1993, Streimann 53091 (CANB). Border Ranges, Lions Road, 32 km west-north-west of Kyogle, 28°21'S, 152°58'E, 360 m, 1998, Streimann 60851, 60856 (CANB, hb. Lücking), 60857 (CANB); *ibid.*, Brindle Creek, 28 km north-north-east of Kyogle, 28°23'S, 153°07'E, 870 m, 1998, Streimann 61149A (CANB); *ibid.*, Pinnacle Hill, 22 km north-east of Kyogle, 28°25'S, 153°07'E, 910 m, 1998, Streimann 61238 (CANB, hb. Lücking). Tooloom Nature Reserve, 28°30'S, 152°23'E, 660 m, 1998, Streimann 60989 (CANB). Victoria Park Nature Reserve, 28°54'S, 153°25'E, 100 m, 1998, Streimann 60736 (CANB). Cedar Park, Tamban Forest Drive, 30°55'S, 152°49'E, 1992, Elix 33154 (CANB). Rawson Falls, 31°37'S, 152°25'E, 460 m, 1998, Streimann 61542 (CANB, hb. Lücking). Currowan State Forest, 35°35'S, 150°03'E, 100 m, 1989, Elix 22765 (CANB). Rutherfords Creek, 36°34'S, 149°36'E, 850 m, 1994, Elix & Kalb 40816 (CANB). Queensland: Wrights Creek, Lake Eacham National Park, 17°16'S, 145°38'E, 680 m, 1994, Streimann 54001A (CANB).

***Gyalectidium minus* Sérus. sp. nov.**

(Fig. 28)

A *Gyalectidio caucasicum* rotundata vel lobata margine, hyphophoribus triangularibus vel laciniatis differt. Typus: SPAIN. Canary Islands, Tenerife: Las Montanas de Anaga, track to Cabezon del Tejo, via Chinobre

and Roque de Anambro, 700–800 m, 1997, Sérusiaux s.n. (LG, holotypus).

Description. THALLUS forming very small, angular-rounded to lobate patches 0.3–1.5 mm diam., areolate-bullate and sometimes rather convex, due to strong encrustation with a continuous layer of crystals, silvery to whitish grey, sometimes with thin greenish parts at the margin. HYPHOPHORES submarginal to marginal, their scales small, emerging from a slightly inflated crystalline bulge, obliquely orientated, triangular to irregularly laciniate, 0.07–0.1 mm long and 0.1–0.2 mm broad, bluish grey when young and becoming whitish translucent when old. APOTHECIA rare, 1–3(–4) per thallus patch, 0.1–0.15 mm diam., with pale orange or pinkish to dark greyish disc and slightly prominent, whitish margin. ASCOSPORES not found (all examined apothecia being immature). PYCNIDIA not found.

Notes. At first glance, *Gyalectidium minus* appears as a reduced or depauperate form of *G. caucasicum*, but detailed examination demonstrates that the populations dealt with here represent a distinct taxon: the rounded or lobate margins of the tiny and convex thallus patches, the shape and colour of the hyphophore scales, as well as the colour of the apothecial disc are diagnostic. Still, the general similarity between *G. minus* and *G. caucasicum* and the absence of the latter in western Europe suggests a vicariance relationship.

Gyalectidium minus is often attacked by the hyphomycete *Hansfordiellopsis lichenicola* (Batista & Maia) Deighton, which obviously is able to alter its vigour.

Distribution and ecology. *Gyalectidium minus* is found in the Canary Islands (Tenerife and Gomera) and southern Italy. In the Italian locality (described in details by Puntillo *et al.*, 2000), it is restricted to leaves of *Buxus sempervirens* while the other *Gyalectidium* species present in the same site (*G. puntilloi*) grows on leaves of *Hedera helix* and *Laurus nobilis*.

Additional specimens examined. ITALY. Campania: Salerno, Morigerati, Grotte del Bussento, 1997, Puntillo 10307, 10390, 10392 (CLU, LG). SPAIN. Canary Islands, Gomera: Trail from Chorros de Epina towards Presa de Los Gallos, 700–800 m, 1994, Sérusiaux s.n. (LG). Garagonay National Park, 1000 m, 1994, Sérusiaux s.n. (LG). Tenerife: Monte de Las Mercedes, near Pico del Ingles, 600–700 m, 1991, Sérusiaux s.n. (LG); *ibid.*, Punta de Anaga, after El Bailadero, 800–900 m, 1991, Sérusiaux s.n. (LG).

***Gyalectidium novoguineense* Sérus. sp. nov.**

(Fig. 32)

A *Gyalectidio flabellato* hyphophoribus anguste triangularibus vel setiformibus differt. Typus: PAPUA

NEW GUINEA. Madang: between Awar plantation and Boroï, 4°06'S, 144°48'E, sea level, 1980, Demoulin 5956 & Smeets (LG, holotypus).

Description. THALLUS forming minute, dispersed to confluent, irregular patches 0.3–0.5 mm diam., together forming an aggregate of up to 5 mm diam., thinly areolate-bullate due to strong encrustation with an irregular to continuous layer of crystals, silvery to whitish grey but sometimes with thin greenish thallus parts at the margin. HYPHOPHORES marginal, their scales small, horizontally arranged, very narrowly triangular, 0.07–0.15 mm long and 20–50 µm broad at the base, whitish to pale grey. APOTHECIA rare, 1(–3) per thallus patch, angular-rounded, 0.2–0.3 mm diam., with greyish to pale yellowish brown disc and slightly prominent, whitish margin that usually has a thin brownish line on the inner side. ASCOSPORES ellipsoid-ovoid, 40–50 × 20–30 µm. PYCNIDIA not found.

Notes. *Gyalectidium novoguineense* belongs to the *G. caucasicum* group and forms a part of a series that goes from broadly flabelliform hyphophores of *G. flabellatum* to the marginal, cilia-like ones of *G. ciliatum*. *G. novoguineense* resembles the latter in its minute scales but differs in their narrowly triangular shape and their horizontal orientation. It could more easily be confused with *G. australe*, which has liguliform (and not triangular) small hyphophores.

Distribution and ecology. Known from low elevation sites (either in pristine rainforest or in artificial habitats) along the northern coast of Papua New Guinea, from south-west Australia and New Caledonia.

Additional specimens examined. PAPUA NEW GUINEA. Madang: Between Awar plantation and Boroï, 4°06'S, 144°48'E, sea level, 1980, Demoulin & Smeets 5889 (LG, topotypus). Mt Baiteta, 55 m, 1989, De Sloover 89L26 (LG). Morobe: Lae, Botanical Garden, 1987, De Sloover 87L56 (LG). AUSTRALIA. New South Wales: Border Ranges, Lions Road, 28°21'S, 152°58'E, 360 m, 1998, Streimann 60851, 60856 (CANB, hb. Lücking), 60857 (CANB). NEW CALEDONIA. Sud: Noumea, I. 1887, Savès 66b. 68 (G). Monts Koghis-Dumbéa, 22°14'S, 166°30'E, 550 m, 1994, Kalb & Kalb s.n. (hb. Kalb).

Gyalectidium palmicola Farkas & Vězda
(Fig. 22)

Farkas & Vězda, Folia Geobot. Phytotax., Praha, 28: 326 (1993). Typus: CUBA. Botanical Garden of Havana, 1990, Farkas s.n. (VBI, holotypus!; Vězda, Lich. Rar. Exs. 93, isotypi).

Description. THALLUS made or irregular, dispersed patches 0.5–2 mm diam., distinctly areolate, with whitish, aplanate, polygonal crystalline clusters separated or surrounded by thin greenish thallus parts. HYPHOPHORES marginal, their scales well-developed, emerging from reniform to crescent-shaped crystalline bulges which develop at the margin of enlarged and distinctly swollen parts of the thallus which are connected to its main part via narrow lobes, horizontally orientated, broadly squamiform and with the upper margin coarsely dentate, 0.1–0.2 mm long and 0.3–0.4 mm broad, whitish translucent to pale greyish or rarely dark brown. APOTHECIA rounded, 2–4(–6) per thallus patch, 0.1–0.2 mm diam., with greyish, slightly pruinose disc and whitish margin (which usually is radially dissected). ASCOSPORES ellipsoid, 30–45 × 10–15 µm. PYCNIDIA not found.

Notes. This species is a typical representative of sect. *Areolectidium*. Its thallus closely resembles that of *G. areolatum*, but its hyphophore scales are distinctive as they are conspicuously dentate and horizontally orientated. The species also resembles *G. flabellatum* which has equally broad but blunt hyphophore scales lacking a distinct crystalline bulge at their base, and an areolate-bullate thallus with an almost continuous layer of crystals.

Distribution and ecology. Known only from the type locality, in a completely artificial vegetation. The species has not been found in the large collections of foliicolous lichens now available from Central and South America and the Caribbean (especially Costa Rica, the West Indies, Ecuador, the Guianas, Brazil and Argentina). It may be endemic to Cuba but its natural habitat remains to be discovered.

Gyalectidium puntilloi Sérus. sp. nov.
(Fig. 21)

A *Gyalectidio areolato* hyphophoribus minoribus, distortis et irregulariter laciniatis differt. Typus: ITALY. Campania: Salerno, Morigerati, Gole del Bussento, 100 m, 1997, Puntillo 10470 (LG, holotypus; CLU, isotypus).

Description. THALLUS forming rounded or irregular patches 1–2(–3) mm diam., distinctly areolate, with whitish, aplanate, polygonal crystalline clusters separated or surrounded by thin greenish thallus parts. HYPHOPHORES submarginal, their scales small, emerging on the outer edges of crystalline areoles, obliquely orientated, squamiform but usually distorted and irregularly lacinate, 0.05–0.08 mm long and 0.07–0.15 mm broad, pale greyish or whitish, sometimes with a bluish tinge at their base. APOTHECIA very

rare, rounded, 0.1–0.2(–0.25) mm diam., with pale or brownish disc and prominent, whitish to grey margin. ASCOSPORES not found. PYCNIDIA not found.

Notes. It is interesting to note that the closest relative of *Gyalectidium puntilloi* is the neotropical *G. areolatum*: both share the same thallus with large, irregular and whitish areoles forming a sharp contrast with the greenish, crystals-free parts. Their hyphophores are diagnostic: in *G. areolatum*, they are typically squamiform, rather large and with two, acute lateral projections, while in *G. puntilloi*, they are usually distorted and lacinate and much smaller.

In Italy, *Gyalectidium puntilloi* is often attacked by the hyphomycete *Hansfordiellopsis lichenicola* (Battista & Maia) Deighton, which obviously is able to alter its health.

The species is named after our colleague and friend, Dr Domenico Puntillo, who has made a great contribution to the study of the lichen flora and vegetation of southern Italy, and who made large collections of this species available to us.

Distribution and ecology. *Gyalectidium puntilloi* is restricted to Europe as it has been found only on both sides of the Pyrenees (France and Spain) and in southern Italy (Campania). In the Pyrenees, it grows on *Buxus sempervirens* leaves and is rather abundant in several small and very humid valleys on the northern side of the range, while in Italy, it has been found in a single locality where it is abundant and grows on leaves of *Hedera helix* and *Laurus nobilis*. This locality has been described in detail by Puntillo *et al.* (2000).

Additional specimens examined. FRANCE. Pyrénées-Atlantiques: Ste-Engrâce, Gorges de Kakouetta, 1989, Sérusiaux s.n. (LG). Pédestarrès, north-west du Pic de Merdanson, 550 m, 2000, Sérusiaux s.n. (LG, hb. Lücking). Hautes-Pyrénées: Ste-Pé-de-Bigorre, west of Lourdes, 380–400 m, 1989 & 2000, Sérusiaux s.n. (LG). SPAIN. Navarra: Hoz de Arbayun, 500–550 m, 1991, Sérusiaux s.n. (LG). Catalunya: Girona, Oix, Riera d'Oix, 500 m, 1991, Diederich (LG); *ibid.*, 1996, Sérusiaux s.n. (LG). ITALY. Campania: Salerno, Morigerati, Gole del Bussento, 100 m, 1997, Puntillo 10476, 10601 (CLU, LG, topotypes).

Gyalectidium radiatum G. Thor, Lücking & Matsumoto (Fig. 17)

In Thor *et al.*, *Symb. Bot. Ups.* 32(3): 43 (2000). *Typus:* JAPAN. Amami-Oshima (Kyushu, Amami Islands, Kagoshima Pref.): 7 km south-west of Nishinakama village, 129°21'E, 28°13'N, 60–80 m, 1995, Thor 13005 (TNS, holotypus!; UPS, isotypus!).

Description. THALLUS forming rounded patches 1–2 mm diam., finely rugose, with verrucae arranged in radiate ridges, greenish to greyish. HYPHOPHORES laminal, their scales well-developed, usually emerging from a crescent-shaped, whitish, crystalline bulge, obliquely orientated, triangular, 0.15–0.25 mm long and 0.1–0.15 mm broad at their base, whitish translucent. APOTHECIA rounded, 0.2–0.3 mm diam., with yellowish green disc and whitish margin. ASCOSPORES ellipsoid-ovoid, 35–50 × 15–20 µm. PYCNIDIA not found.

Notes. *Gyalectidium radiatum* is closely related to *G. verruculosum* from which it differs by the radiate thallus ridges. This feature is unique among *Gyalectidium* and within the Gomphillaceae is otherwise only known from *Actinoplaca strigulacea* Müll. Arg.

Distribution and ecology. *Gyalectidium radiatum* is a very rare species, being known from only two distinct localities, one in southern Japan and the other one in the south-western Pacific, in the Vanuatu archipelago.

Additional specimens examined. VANUATU. Espiritu Santo: Mt Malel, 15°15'S, 167°06'E, 180 m, 1998, Streimann & Ala 62259B (CANB, hb. Lücking).

Gyalectidium setiferum Vězda & Sérus.
(Fig. 40)

In Sérusiaux, *Nord. J. Bot.* 13: 454 (1993). *Typus:* GEORGIA. Colchis: Soci, valley of Chosta river, 50 m, 1980, Vězda s.n. (hb. Vězda, holotypus!).

Description. THALLUS forming rounded to irregular, single or dispersed patches forming aggregates 1–4 mm diam., finely verrucose, pale greenish to whitish grey, with scattered sterile setae on the thallus that resemble those of the hyphophores. HYPHOPHORES laminal, their scales completely divided into a circle of 2–6 vertically orientated cilia surrounding the greenish or rarely yellowish brown, distinctly prominent, swollen diahyphal mass, 0.3–0.5 mm long, tapering towards the tips, translucent to whitish but dark, especially at tips, on old thalli. APOTHECIA and PYCNIDIA not found.

Notes. *Gyalectidium setiferum* is usually lacking in vigour but quite easy to recognize; indeed, it has scattered cilia and hyphophores reduced to a circle of cilia surrounding the swollen diahyphal mass. The scattered cilia can be interpreted as poorly developed hyphophores which fail to produce diahyphae. *G. eskucheii* is externally similar but lacks sterile setae, and its hyphophores are divided into narrowly triangular lobes that are regularly arranged in a circle enclosing an adnate, dark greyish brown diahyphal mass. Sterile setae are otherwise only known from *G. microcarpum*,

which differs in the coarsely verrucose thallus lacking hyphophores.

Distribution and ecology. *Gyalectidium setiferum* is known only from Europe, in the western part of the Caucasus (Russia and Georgia), on both sides of the Pyrenees (France and Spain), as well as in a single locality further north in Brittany (western France). The species can grow on needles of *Abies alba* (Brittany) or *A. nordmanniana* (western Caucasus), on leaves of *Buxus* (either *B. sempervirens* in the Pyrenees or *B. colchica* in western Caucasus) and *Laurocerasus officinalis* (western Caucasus).

Specimens examined. See Sérusiaux (1993).

***Gyalectidium verruculosum* Sérus. sp. nov.**

(Fig. 16)

A *Gyalectidio filicino* hyphophoribus triangularibus, in parte basali e verruca crystallina lunata emergentibus differt. Typus: PAPUA NEW GUINEA. Madang: Brahman Mission, southern side of Ramu river, 5°54'S, 145°20'E, 100 m, 1995, Sérusiaux 15701 (LG, holotypus).

Description. THALLUS forming rounded patches 2–5 mm diam., finely verrucose, pale greenish to greyish. HYPHOPHORES laminal, their scales well-developed, usually emerging from a crescent-shaped, whitish, crystalline bulge, obliquely to almost horizontally orientated, triangular, 0.15–0.25 mm long and 0.1–0.15 mm broad at their base, whitish translucent to pale greyish, rarely with a bluish tinge. APOTHECIA rare but usually numerous on certain thalli, angular-rounded, 0.15–0.25 mm diam., with pale yellowish brown to greenish grey, slightly pruinose disc and whitish margin. ASCOSPORES ellipsoid, 25–35 × 10–15 µm. PYCNIDIA not found.

Notes. *Gyalectidium verruculosum* is easily identified by its hyphophores, as the triangular scale typically develops at the inner side of a crescent-shaped bulge on the thallus surface. Most similar are *G. radiatum*, in which the thallus verrucae are radially elongated, and *G. laciniatum*, which has lacinate hyphophore scales.

Distribution and ecology. Known from the lowland forest along the northern coast of Papua New Guinea where it occurs together with *Gyalectidium caucasicum* and *G. flabellatum*; also recorded from several localities in Australia (Queensland and New South Wales) and from the Vanuatu archipelago. The species is probably quite abundant in Australasia but may have been mistaken for *G. filicinum*.

Additional specimens examined. PAPUA NEW GUINEA. Madang: Brahman Mission, 5°54'S, 145°20'E, 100 m, 1995, Sérusiaux 15808 (LG, topotypes). AUSTRALIA. Queensland: Wrights Creek, Lake Eacham National Park, 17°16'S, 145°38'E, 680 m, 1994, Streimann 54014A (CANB). Curtain Fig Tree State Forest Park, 17°17'S, 145°34'E, 700 m, 1994, Streimann 54029A (CANB, hb. Lücking). New South Wales: Macquarie Pass National Park, 34°34'S, 150°41'E, 80 m, 1993, Streimann 53091 (CANB). Murray Scrub Forest Reserve, 28°29'S, 152°46'E, 750 m, 1998, Streimann 60793 (CANB). Border Ranges, Lions Road, 28°21'S, 152°58'E, 360 m, 1998, Streimann 60851 (CANB, hb. Lücking), 60856, 60857 (CANB). VANUATU. Espiritu Santo: Mt Malel, 15°15'S, 167°06'E, 180 m, 1998, Streimann & Ala 62259B (CANB).

***Gyalectidium yahriae* Buck & Sérus.**

(Fig. 25)

Buck & Sérusiaux, *Bryologist* 103: 134 (2000). Typus: U.S.A. Florida: Manatee County, Duette Park, 27°32'N, 82°06'W, 1998, Buck 33988 (NY, holotypus!).

Description. THALLUS corticolous on small twigs and overgrowing a green, powdery algal layer, forming small, rounded, single or confluent patches 3–6 mm diam., typically smooth and lacking crystals but sometimes with irregular verrucae, greenish grey to dark green. HYPHOPHORES laminal, their scales well-developed, vertically orientated, formed by a circle of 10–17 narrowly triangular, contiguous lobes being slightly curved outwards except in old hyphophores, 0.2–0.25 mm long, the whole circle 0.2–0.25 mm diam., whitish to pale greyish. Diahyphae easily seen at early stages of development as a central mass, soon appearing as strings of beads, under the microscope with each cell strongly inflated and *c.* 2–3(–3.5) × 2(–2.2) µm; smaller and rounded (20–25 µm diam.) masses eventually individualizing and moving apart from each other because of the growth of long cilia (8–12 µm) out of their edge cells; these masses representing single diaspores. APOTHECIA and PYCNIDIA not found.

Notes. Although its hyphophores can be regarded as similar to those of *Gyalectidium eskucheii*, for example, the position of this species in *Gyalectidium* might be questioned. Indeed, there are two differences from all other *Gyalectidium* species regarding the diahyphal mass: the individual cells of the diahyphae are shorter and inflated, and their edge cells produce long cilia. These differences might be related to the function of the hyphophores which indeed seem to act like soralia, the single diahyphal balls that are separated by the cilia working as soredia. In this way, *G. yahriae* forms

an interesting parallel to species such as *Gyalideopsis anastomosans* P. James & Vězda and allies, *G. hyalina* Lücking, *Actinoplaca strigulacea* Müll. Arg., and *Echinoplaca gemmifera* Lücking. In these species, the hyphophores are strongly derived to resemble genuine isidia or even campylidia. In *Echinoplaca gemmifera*, however, which has disc-shaped diahyphal masses resembling isidia, the apothecia are absolutely identical with those of *E. pellicula*, which has typically setiform hyphophores. Thus, the particular hyphophores of *Gyalectidium yahriae* are well within the variational range to be expected within a genus, considering the fast evolution found in hyphophores within the Gomphillaceae.

The general shape of the hyphophores is diagnostic for *Gyalectidium yahriae*: at least when young, they look like flower vases with a dentate edge. The material from Florida is well-developed and the above description is based on it; the specimens from Papua New Guinea are rather depauperate and show small discrepancies but, with the material at hand, we see no reason to consider both populations as not conspecific.

Distribution and ecology. *Gyalectidium yahriae* is a rare species, known from Florida (USA) and Papua New Guinea. In Florida, it grows in xeromorphic shrub vegetation communities dominated by evergreen oaks, often with a sparse pine overstory, or in more humid stands. In Papua New Guinea, it has been found on bark and decorticated wood in open grassland or at the margins of montane forest. *G. yahriae* is the only typically corticolous species of the genus known so far.

Specimens examined. See Buck & Sérusiaux (2000).

Gyalectidium sp. A

Description. THALLUS forming rounded patches 1–3 mm diam., thinly verrucose to almost smooth, greenish to whitish grey. HYPHOPHORES submarginal, their scales well-developed, emerging centrifugally from semi-circular crystalline bulges, obliquely orientated, divided into 2–3 narrowly triangular, partly bent and twisted segments, 0.2–0.3 mm long and 0.2–0.3 mm broad at the base, whitish translucent to pale greyish. APOTHECIA rounded, flat, 0.2–0.3 mm diam., with dark greyish brown, distinctly pruinose disc and dark greyish brown margin. ASCOSPORES oblong-ellipsoid, 35–50 × 12–20 µm. PYCNIDIA not found.

Notes. This taxon is known from two rather scanty but uniform collections. It appears intermediate between *Gyalectidium caucasicum* and *G. kenyanum*. As in the latter, its hyphophore scales emerge submarginally from crystalline bulges and are obliquely orientated,

but are here clearly divided into 2–3 segments. Furthermore, the thallus is thinner than in *G. caucasicum*, and the apothecia are darker and comparatively flat. The divided hyphophore scales resemble those of *G. kenyanum*, but in the latter they are much narrower, more numerous and arranged in a circle emerging from a ring-shaped bulge in which the diahyphal mass is immersed. *Gyalectidium* sp. A cannot be identified with any of the taxa described above, but the available material is too scanty to justify a formal description at present.

Specimens examined. COSTA RICA. Heredia: La Selva Biological Station, 10°26'N, 84°03'W, 50–100 m, 1997, Lücking 97-1285 (hb. Lücking). ARGENTINA. Misiones: Depto. Guaraní, 1500 m, 1994, Maruñak 735 (hb. Lücking).

EXCLUDED SPECIES

Gyalectidium aff. *caucasicum* (Elenk. & Woron.) Vězda

Malcolm & Vězda, Australas. Lichenol. Newsletter 40: 18 (1997). NEW ZEALAND. South Island: Marlborough, Pelorus Bridge, 41°18'S, 173°34'E, 55 m, mixed *Podocarpus-Nothofagus* forest, 1995, Malcolm 2297, 2318-2321, 2339 (hb. Malcolm).

Malcolm & Vězda (1997) compared those collections (made on living leaves and on bark) with *G. caucasicum* but indicated that they differ by their marginally lobulate thallus and the presence of traces of usnic acid and two unknown substances. We have not examined the material and thus are unable to comment further on their taxonomical status.

Gyalectidium corticola Henssen

Henssen, Lichenologist 13: 156 (1981). Typus: COSTA RICA. Puntarenas: Monteverde Cloud Forest Reserve, 10°18'N, 84°50'W, 1500 m, montane rain forest, corticolous, 1979, Henssen 26251 (MB, holotypus).

This species has been included in the genus *Gyalectidium* by Henssen (1981) because of the corticate thallus, the thalline apothecial margin, the presence of epithelial algae, and the single, muriform ascospores. As outlined above, epithelial algae and muriform ascospores can no longer be considered as apomorphies of *Gyalectidium*, since they also occur in *Calenia* and other genera, e.g. *Gyalideopsis vulgaris* (Lücking, 1997). The apothecia in *G. corticola* are very large and covered by triangular lobes, very much as in certain species of *Calenia*, *Asterothyrium* and *Ocellularia*, but unknown in *Gyalectidium* s.s. Furthermore, the characteristic hyphophores have not been found in that species. We are therefore convinced that *G. corticola* does not belong to the genus, which is

confirmed by the phylogenetic analysis where the species falls within *Calenia* (Fig. 7), and with the present generic delimitation in the Gomphillaceae, it is best included in that genus. We therefore introduce the new combination *Calenia corticola* (Henssen) Ferraro, Lücking & Sérusiaux. **comb. nov.** (Bas.: *Calenia corticola* Henssen, *Lichenologist* 13: 156, 1981).

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