

Additions and corrections to the knowledge of the foliicolous lichen flora of Costa Rica.

The genus *Fellhanera*, with notes on *Bacidia pauciseptata*

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Abstract: This further contribution to the knowledge of the foliicolous lichen flora of Costa Rica provides a detailed account on the genus *Fellhanera*. In total, 25 species and five undescribed taxa are treated. Ten species are described as new: *Fellhanera angustispora* sp.n., *F. dictyospora* sp.n., *F. dispersa* sp.n., *F. emarginata* sp.n., *F. pilomarginata* sp.n., *F. longispora* sp.n., *F. muhlei* sp.n., *F. montana* sp.n., *F. verrucifera* sp.n., and *F. viridis* sp.n. New combinations are *F. pauciseptata* (R. Sant.) R. Lücking comb.n. [Bas.: *Bacidia pauciseptata* R. Sant.] and *F. rubida* (Müll. Arg.) R. Lücking comb.n. [Bas.: *Patellaria rubida* Müll. Arg.]. *F. dominicana* (Vain.) Vezda is placed into synonymy with *F. fuscatula* (Müll. Arg.) Vezda, whose type has 7-septate ascospores, and the name *F. subfuscatula* R. Lücking sp.n. is introduced for the taxon with 5-septate ascospores formerly known as *F. fuscatula*. *F. misionensis* Ferraro & R. Lücking ined. and *F. sublecanorina* (Nyl.) Vezda are reported for the first time from Costa Rica. The formerly invalidly published names *F. farinosa* nom. nud. and *F. pilosa* nom. nud. are considered to be synonyms of *F. fuscatula* (Müll. Arg.) Vezda and *F. rhabdophylli* (Rehm) Vezda, respectively. Specimens identified as *F. tuckeri* nom. nud. belong to *F. rhabdophylli* as well. *F. buxi* is excluded from the foliicolous lichen flora of Costa Rica. A key is provided to the complex group of species of *Fellhanera* with brownish apothecia and 3-septate ascospores. Infrageneric relationships within *Fellhanera* are briefly discussed, and notes on the ecology of the species are provided.

Resumen: La presente contribución al conocimiento de la líquenoflora foliícola de Costa Rica trata en detalle el género *Fellhanera*, incluyendo 25 especies y otros cinco taxa aún no descritos hasta la fecha. Se describen diez especies nuevas: *Fellhanera angustispora* sp.n., *F. dictyospora* sp.n., *F. dispersa* sp.n., *F. emarginata* sp.n., *F. pilomarginata* sp.n., *F. longispora* sp.n., *F. muhlei* sp.n., *F. montana* sp.n., *F. verrucifera* sp.n., y *F. viridis* sp.n., además de las nuevas combinaciones *F. pauciseptata* (R. Sant.) R. Lücking comb.n. [Bas.: *Bacidia pauciseptata* R. Sant.] y *Fellhanera rubida* (Müll. Arg.) R. Lücking comb.n. [Bas.: *Patellaria rubida* Müll. Arg.]. *F. dominicana* (Vain.) Vezda es puesta en sinonimia con *F. fuscatula* (Müll. Arg.) Vezda, cuyo material tipo tiene esporas 7-septadas, y el nombre *F. subfuscatula* R. Lücking sp.n. es introducido para el taxon con esporas 5-septadas, hasta ahora conocido como *F. fuscatula*. *F. misionensis* Ferraro & R. Lücking ined. y *F. sublecanorina* (Nyl.) Vezda son comunicados por primera vez de Costa Rica. Los nombres *F. farinosa* nom. nud. and *F. pilosa* nom. nud., invalidamente publicadas por el autor en una publicación anterior, son considerados como sinónimos de *F. fuscatula* (Müll. Arg.) Vezda y *F. rhabdophylli* (Rehm) Vezda, respectivamente. Especímenes entonces identificados como *F. tuckeri* nom. nud. actualmente pertenecen a *F. rhabdophylli*; igualmente, *F. buxi* Vezda & Vivant es excluida de la líquenoflora foliícola de Costa Rica. Se presenta una clave para el difícil grupo de especies de *Fellhanera* con apotecios marrones y esporas 3-septadas. Finalmente, se discuten las relaciones infragenericas dentro del género *Fellhanera*, y se dan notas sobre la ecología de las especies.

INTRODUCTION

Introduced as a segregate of *Bacidia* De Not. (Vezda 1986), *Fellhanera* Vezda is characterized by biatorine apothecia with paraplectenchymatous exciple, ascus of the *Byssoloma* type, combined with *Bilimbia* type ascospores, and bacillar or pyriform pycnosporos. In his monograph on the foliicolous lichens, Santesson (1952) treated, among *Catillaria*, *Bacidia* and *Lopadium*, only ten species later to be referred to *Fellhanera*, whereas Vezda (1986) already accepted 19 taxa. Recently, Sérusiaux (1996) provided a key to the foliicolous taxa, including no less than 33 species. The rapidly increasing knowledge on the diversity of the genus *Fellhanera* is further demonstrated by the present paper, in which 25 foliicolous taxa known from Costa Rica are treated, 10 of which are new to science, and another five still left undescribed. Three further new species, *F. badimioides* R. Lücking, Lumbsch & Elix, *F. avilezii* R. Lücking, and *F. misionensis* Ferraro & R. Lücking ined., were already described in other papers or are about to be published (Lücking et al. 1994; Lücking & Lücking 1995; Ferraro & Lücking, in prep.). Together with *F. avilezii* and *F. winkleriana* R. Lücking (Lücking 1991, 1992a), which are not treated in the present paper, the foliicolous lichen flora of Costa Rica now comprises 27 species, plus a number of still undescribed taxa.

Substantial increase of the number of species to be assigned to *Fellhanera* could be expected by revision of non-foliicolous material, either by species already described under other generic names, such as *Catillaria* and *Bacidia*, or by unknown taxa yet to be described. However, a preliminary survey of specimens housed in B, G, and UPS, as well as examination of fresh collections gathered by the author in different tropical areas (Costa Rica, Guyana, Ecuador) indicates that corticolous or saxicolous species with features typical of *Fellhanera* are less common than foliicolous ones or belong to otherwise foliicolous species, such as *Fellhanera bouteillei* (Desm.) Vezda (Santesson 1952). Obviously, the appropriate habitats in which corticolous and saxicolous species of *Fellhanera* would be expected, and are actually found, such as the shady understory of wet tropical forests, are largely dominated by other taxa with much larger thalli and apothecia,

e.g. *Lecidea* s.l., *Bacidia* spp., *Bacidina* spp., and some Thelotremataceae. Interestingly, many of these taxa, although belonging to a variety of non-related genera, usually resemble the genus *Fellhanera* externally by their greenish, granulose thalli and their brownish apothecia.

The chemistry of *Fellhanera* was studied in detail by Lücking et al. (1994), though secondary compounds had been reported from *F. bouteillei* before (Tønsgberg 1992). Generally, taxa with bluish thalli have secondary compounds, whereas species with greenish thalli do not, underlining the taxonomic importance of thallus colour. Based on morphological, anatomical and chemical characters, the 44 foliicolous representants of the genus *Fellhanera* can be divided into various groups, which are in part natural and reflect separate evolutionary lines, and in part artificial, representing convergent evolutionary development. With some few exceptions, further generic delimitation on the basis of these groups seems impossible, since the genus as a whole is rather homogeneous. At best, some groups can be addressed on the subgeneric level. In order to facilitate access to the enormous diversity within *Fellhanera*, a short account on infrageneric relationships is given at the end of this paper.

MATERIAL AND METHODS

The study area is described in detail in earlier papers (Lücking 1992a, c, 1995a) and in the first contribution to the present series (Lücking 1995b). Microscopic investigations and ascospore measurements were made in tap water.

THE SPECIES

The taxa are listed alphabetically, following the nomenclature of Santesson (1952), Lücking (1992a) and Farkas & Sipman (1993). Nomenclatural references are only given if deviating from Farkas & Sipman (1993). Species new to the foliicolous lichen flora of Costa Rica are marked with an asterisk. Two species, *Fellhanera winkleriana* and *F. avilezii*, which were already included in two former floristic treatments of Costa Rica (Lücking 1992a) and Cocos Island (Lücking & Lücking 1995), are omitted here, since no new data or

collections were available. New collections are given for some rare species, viz. *F. elliottii*, *F. lisowskii*, and *F. subternella*, while *F. badimioides*, described and extensively treated by Lücking et al. (1994), is included for the sake of completeness. If not otherwise stated, the cited specimens were collected by the author. The main sets of specimens are deposited in CR and the herbarium of the author, whereas duplicates have been distributed among the following herbaria: B, BM, CBG, G, GZU, LG, M, NY, STU, ULM, UPS, VBI, hb. Kalb, hb. Vezda.

Fellhanera angustispora R. Lücking sp.n. (Fig. 1 A-C)

Thallus epiphyllus, tenuissimus, continuus, laevigatus, viride cinereus. Apothecia 0.15-0.25 (-0.3) mm diam., rotundata, convexa, fusca, emarginata. Excipulum indistinctum. Hypothecium fuscum. Hymenium incoloratum. Paraphyses ramoso-connexae. Asci clavati, ad typum *Byssoloma* pertinentes. Ascospores 8-nae, 3-septatae, anguste fusiformes, 10-16 × 2-3 μm. Alga ad Chlorococceas pertinet.

Typus: COSTA RICA. Heredia: La Selva Protection Zone, 10° 26' N, 84° 03' W, 50-100 m, primary lowland rain forest on CES/LOC/CEN trails, on leaves of a palm, IX. 1991, leg. R. Lücking 91-4932 (ULM holotype).

Description: Thallus epiphyllous, thin, continuous, smooth, pale greenish grey. Phycobiont a species of Chlorococceae, cells 4-8 μm diam.

Apothecia 0.15-0.25 (-0.3) mm diam. and 0.08-0.1 mm high, with a convex, brown disc, emarginate, but with the marginal zone paler than the inner part of the disc. Exciple much reduced and indistinct, even in young apothecia. Hypothecium brown, 20-30 μm high; central apothecial base not well distinguished in colour from the surrounding tissue. Hymenium 45-50 μm high, colourless. Paraphyses 0.07 μm thick, branched and anastomosing. Asci clavate, 40-45 × 10-12 μm, of the *Byssoloma* type. Ascospores 8 per ascus, 3-septate, narrowly fusiform to almost bacillar, colourless, 10-16 × 2-3 μm.

Pycnidia not seen.

Etymology: The name refers to the comparatively narrow ascospores.

Notes: *Fellhanera angustispora* is closely related to *F. emarginata*, another new species described below. As the latter, it is characterized by the much reduced exciple and the rather small, convex, dark apothecia. Both species differ from each other by their thallus colour and ascospore dimensions. *F. angustispora* and *F. emarginata* might be confused with *Byssoloma minutissimum* and its relatives (Kalb & Vezda 1990), which, however, have a byssoid exciple, at least in young apothecia, and their apothecia are usually paler.

The reasons why the new species, in spite of its reduced exciple, is placed in *Fellhanera* instead of *Byssoloma*, are discussed below *F. pilomarginata*.

Additional specimens examined: COSTA RICA. Alajuela: Caño Negro National Wildlife Refuge, 10° 54' N, 84° 47' W, 50 m, isolated primary lowland rain forest, 92-2753 (M). Heredia: La Selva Protection Zone, 10° 26' N, 84° 03' W, 50-100 m, primary lowland rain forest on CES/LOC/CEN trails, 91-4925 (CR); *ibid.*, secondary forest on SOC trail, 91-5607 (LG, NY, UPS, VBI, hb. Kalb); *ibid.*, forest margin near laboratory, 91-2362 (CBG). Cartago: Cervantes, 9° 53' N, 83° 49' W, 1450 m, small relict forest, 91-3831 (B, GZU, STU). Puntarenas: Corcovado National Park, »Los Patos«, 8° 34' N, 83° 31' W, 50-150 m, primary lowland rain forest, 92-3120 (hb. Lücking). Limón: Braulio Carillo National Park, section Quebrada Gonzales, »Botarrama« trail, 10° 12' N, 83° 55' W, 480 m, primary submontane rain forest, 91-1300 (hb. Lücking, with *F. emarginata*). Río Corinto, 10° 12' N, 83° 53' W, 200 m, gallery forest, 92-3946 (hb. Kalb, with *Byssoloma minutissimum*). Tortuguero National Park, Cerro Tortuguero, 10° 35' N, 83° 31' W, 0-100 m, primary lowland rain forest, 92-2570 (LG).

Fellhanera badimioides R. Lücking, Lumbsch & Elix

Lücking, R., Lumbsch, H. T. & Elix, J. A., *Bot. Acta* 107: 400 (1994).

Selected specimens examined: COSTA RICA. Heredia: La Selva Protection Zone, 10° 26' N, 84° 03' W, 50-100 m, primary lowland rain forest on CES/LOC/CEN trails, 91-4934 (hb. Lücking, with *F. lisowskii*). Limón: Hitoy Cerere Biological Reserve,

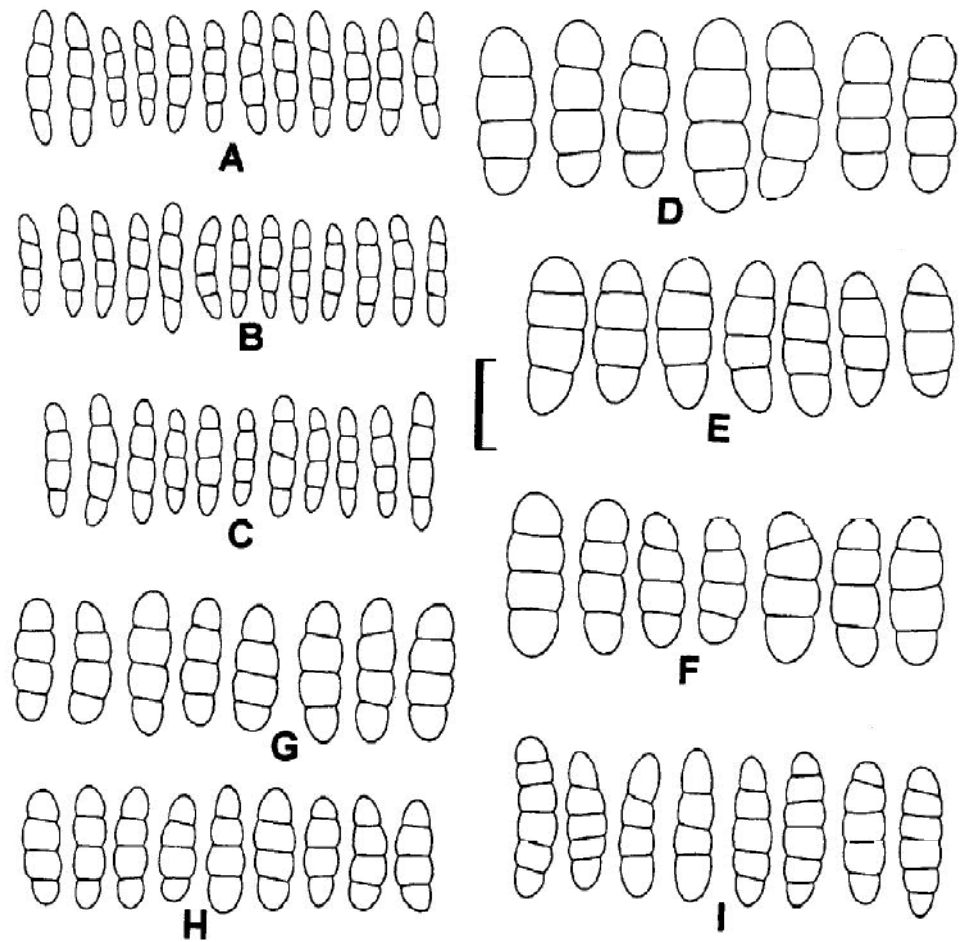


Figure 1. (A-C) *Fellhanera angustispora* [(A) 92-3120, (B) 91-4932, (C) 91-1285]. (D-F) *F. emarginata* [(D) 92-4769, (E) 92-2521, (F) 91-3943]. (G-H) *F. rubida* [(G) 91-5203, (H) 91-2793]. (I) *F. aff. emarginata* [91-3225]. Ascospores. Scale = 10 μ m.

9° 41' N, 83° 02' W, 100-200 m, primary lowland to submontane rain forest, 91-1301 (M holotype; hb. Lücking isotype).

Fellhanera bouteillei (Desm.) Vezda

Notes: The present material demonstrates the extraordinarily variable thallus and apothecial morphology of this species. Thallus colour ranges from pale bluish grey to almost white, and the surface structure from farinose to almost smooth or coarsely granulose. The apothecia are usually thin but may also be thicker and distinctly raised over the thallus surface. The colour of the disc varies from pale yellowish and almost translucent to vividly orange yellow; the margin is often irregular and of the same colour as the disc or whitish. The outer surface of the lateral exciple is often covered with crystals. Coarsely granulose thalli seem to be more frequent in cooler, montane areas, whereas the apothecial colour might depend on light intensity, specimens with darker apothecia being more common in open situations.

Selected specimens examined: COSTA RICA. San José: Chirripó National Park, 9° 28' N, 83° 34' W, 1800-2200 m, primary upper montane rain forest, 92-214 (UPS), 92-251 (NY), 92-311 (ULM); *ibid.*, 9° 28' N, 83° 33' W, 2200-2550 m, 92-338 (CR, STU); *ibid.*, 9° 28' N, 83° 33' W, 3000-3200 m, primary cloud forest below »Hopeless Mountain«, 92-538 (GZU, LG, NY, UPS, hb. Kalb), 92-570 (LG, CBG). Las Quebradas, 9° 26' N, 83° 42' W, 900-1000 m, *Citrus* trees and coffee plantation, 92-4287 (hb. Lücking). Cartago: Alto La Gloria, Interamerican highway, 9° 48' N, 83° 57' W, 1700 m, gallery forest, 91-3625 (CR). Orosi valley, 9° 47' N, 83° 51' W, 1150 m, coffee plantations, 92-2905 (NY). Tapanti National Wildlife Refuge, »La Pava« trail, 9° 46' N, 83° 47' W, 1500-1700 m, primary montane to upper montane rain forest, 92-24 (NY); *ibid.*, 1800 m, forest margin at mirador, 91-3224 (VBI, hb. Kalb). Trinidad, Interamerican highway, 9° 40' N, 83° 53' W, 2550-2600 m, forest margin near road, 91-3507 (UPS), 91-3513 (B, M). Villa Mills, Interamerican highway, 9° 34' N, 83° 42' W, 3000 m, secondary vegetation bordering reforested area, 91-3998 (CR). Limón: Braulio Carrillo National Park, section Quebrada Gonzales, »Botarrama« trail near the Rio Sucio, 10° 12' N, 83° 55' W, 480 m, forest margin, 91-297 (hb.

Kalb). Hitoy Cerere Biological Reserve, 9° 41' N, 83° 02' W, 100 m, forest margin at small river, 91-1280 (hb. Lücking).

Fellhanera dictyospora R. Lücking sp.n. (Fig. 2 B)

Thallus epiphyllus, tenuis, continuus, farinosus, viride cinereus. Apothecia 0.1-0.2 mm diam., rotundata, plana ad leviter convexa, fusca. Excipulum paraplectenchymaticum, incoloratum. Hypothecium fuscum; pars basalis apothecii fusco-nigra. Hymenium incoloratum. Paraphyses ramoso-connexae. Asci clavati. Ascospores singulae, muriformes, ovoideae, 35-40 × 15-20 µm. Alga ad Chlorococcaceas pertinet.

Typus: COSTA RICA. Heredia: La Selva Protection Zone, 10° 26' N, 84° 03' W, 50-100 m, primary lowland rain forest on SOR trail, on leaves of a dicotyledon, IX. 1991, leg. R. Lücking 91-5567 (ULM holotype).

Description: Thallus epiphyllous, thin, continuous, somewhat irregular in outline, farinose, greenish grey to greenish. Phycobiont a species of Chlorococcaceae, cells 5-10 µm diam.

Apothecia 0.1-0.2 mm diam. and 0.1-0.15 mm high, with a plane to slightly convex, brown disc (sometimes with a slight purplish tinge), and a margin of similar colour or darker which is often reduced in mature apothecia. Exciple distinctly paraplectenchymatous, colourless, up to 20 µm broad, cells 3-6 µm diam. Hypothecium dark brown, 15-25 µm high; central apothecial base blackish brown. Hymenium 70-75 µm high, colourless. Paraphyses 0.07 µm thick, branched and anastomosing. Asci clavate, 55-70 × 20-25 µm, I+ blue, no distinct apical structure visible. Ascospores single, muriform, broadly ovoid, colourless, 35-40 × 15-20 µm.

Pycnidia not seen.

Etymology: The name refers to the muriform ascospores.

Notes: In spite of the single, muriform ascospores, a feature hitherto unknown in the genus, *Fellhanera dictyospora* appears to be a genuine *Fellhanera*. Externally, the species is rather similar to *F. rhapsidophylli* or *F. fuscata*. The absence of a tholus of the *Byssoloma* type in the asci is

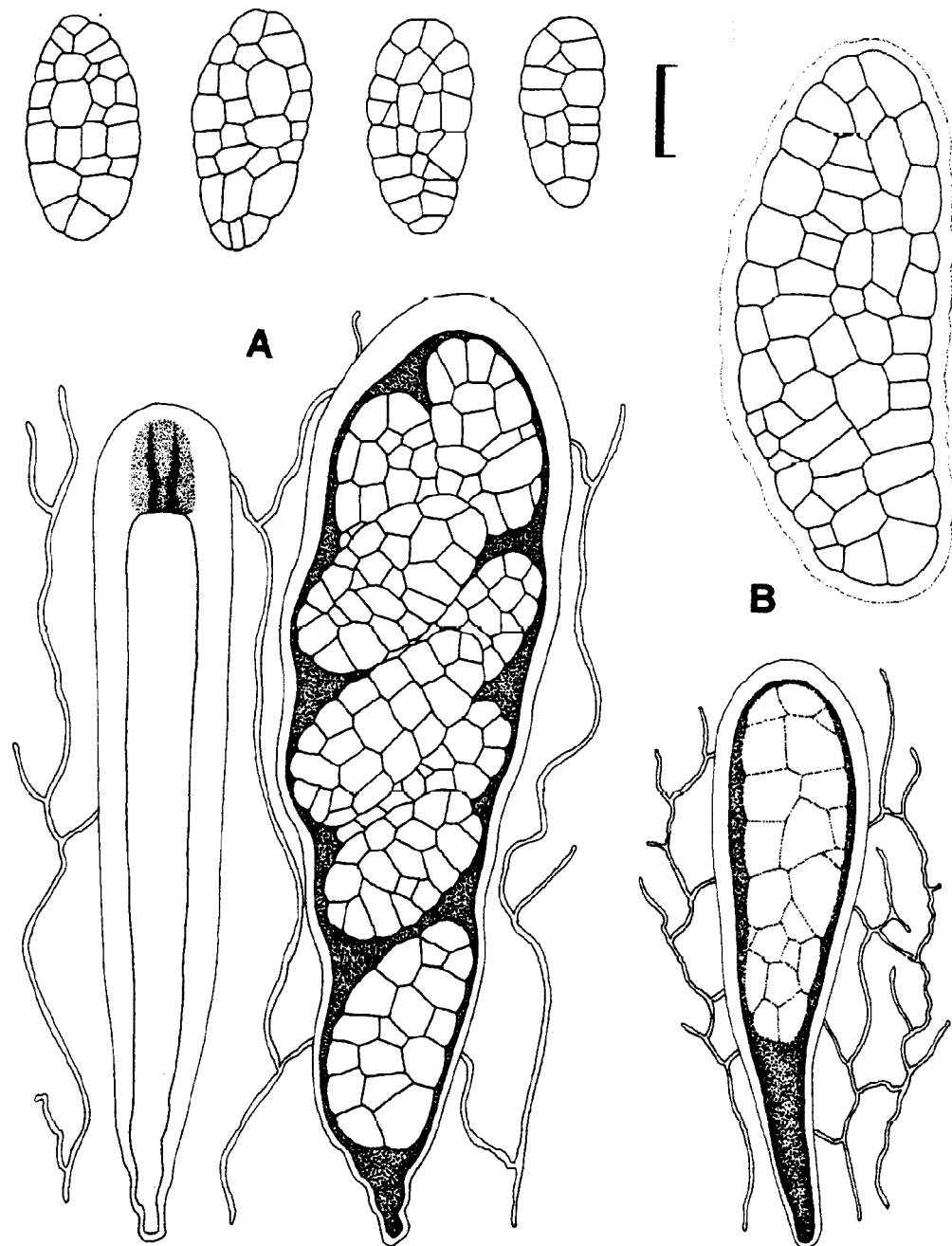


Figure 2. (A) *Fellhanera montana* [holotype]. (B) *F. dictyospora* [holotype]. Asci and ascospores. Scale = 10 μ m.

probably due to the large, single ascospores. A similar variation, correlating with the ascospore type, is found in the genus *Tapellaria* (Lücking, in prep.). As in the latter (Santesson 1952), we now find an almost continuous series from transversely septate to muriform ascospores in the genus *Fellhanera*, particularly in the group of species including the generic type, with brownish apothecia and greenish grey, smooth to farinose thalli.

The large, muriform ascospores of *Fellhanera dictyospora* might raise the question why this species has not been placed in the genus *Calopadia* (see Vezda 1986). Following Santesson's (1952) definition of such genera as *Tapellaria* or *Echinoplaca*, most workers nowadays agree that the concept of ascospore genera, so strictly applied by Zahlbruckner, is ill-defined. Thus, relationships concluded from the ascospore type must be supported by other features; otherwise, the resulting entities are polyphyletic and unnatural. The genus *Calopadia* is clearly circumscribed by a number of characters: the rather large apothecia having very distinct, free, simple or only basally branched paraphyses, the rounded, smooth, pale, dispersed but confluent thallus patches, and the formation of campylidia of the *Pyrenotrichum splitgerberi* type. Any species to be included in *Calopadia* must share these features; otherwise, the generic concept within the core group of the Ectolechiaceae (*Calopadia*, *Tapellaria*, *Lasioloma*, *Sporopodium*) would break down, and natural relationships be obscured.

It is true that *Fellhanera* and *Calopadia* are similar in some respects (brownish apothecia with paraplectenchymatous exciple and aeruginous apothecial base), and there might exist direct or indirect systematic relationships between both genera (see also Lücking et al. 1994). However, except for these similarities, *Fellhanera dictyospora* lacks any character typical of *Calopadia* and on the other hand shares most features characteristic of *Fellhanera* (compare Lücking et al. 1994): the small apothecia in which the margin is reduced in maturity, the indistinct, branched and anastomosing paraphyses, and the continuous, farinose thallus, together with the absence of any signs of campylidia. In fact, the specimens are externally impossible to distinguish from either *F. rhapsidophylli*, *F. subfuscatula*, or *F. fuscatula*.

The differences towards the hitherto known species of *Fellhanera*, i.e. the single, muriform ascospores and the absence of a tube in the tholus of the asci, are minor in this respect, because of the following reasons: (1) With the ascospore variation found in *F. elliottii* and *F. paradoxa*, single muriform ascospores can be expected to occur within the genus; (2) judging from the genus *Tapellaria*, the ascus type of species with single large ascospores regularly deviates from that of species with numerous small ascospores. Therefore, the generic placement of *Fellhanera dictyospora* is justified.

Additional specimens examined: COSTA RICA. Cartago: Guayabo National Monument, 9° 59' N, 83° 43' W, 800-900 m, primary lower montane rain forest, 92-2196 (STU). Limón: Braulio Carillo National Park, section Quebrada Gonzales, »Botarrama« trail, 10° 12' N, 83° 55' W, 480 m, primary submontane rain forest, 91-1309 (hb. Lücking); *ibid.*, canopy layer, 91-1307 (B). Hitoy Cerere Biological Reserve, 9° 41' N, 83° 02' W, 100-200 m, primary lowland to submontane rain forest, 91-1308 (hb. Lücking).

Fellhanera dispersa R. Lücking sp.n. (Fig. 6 B)

Thallus epiphyllus, tenuis, dispersus, laevigatus ad leviter rugosus, albo-viridis. Apothecia 0.25-0.45 mm diam., rotundata, fusco-rubra. Excipulum paraplectenchymaticum, incoloratum. Hypothecium fuscum; pars basalis apothecii fusca. Hymenium incoloratum. Paraphyses ramoso-connexae. Asci clavati, ad typum *Byssoloma* pertinentes. Ascosporae 8-nae, 3-septatae, oblongo-ellipsoideae, 12-15(-17) × 4-4.5 µm. Alga ad Chlorococcaceas pertinentes.

Typus: COSTA RICA. San José: Chirripó National Park, 9° 28' N, 83° 34' W, 1800-2200 m, primary upper montane rain forest, on leaves of Ericaceae, II. 1992, leg. R. Lücking 92-213 (ULM holotype; hb. Lücking isotype).

Description: Thallus epiphyllous, thin, discontinuous, composed of dispersed, up to 1 mm diam. and 15-20 µm thick algiferous patches, smooth or very slightly rugose, sometimes with thin lobes at the margins, whitish green to white, very rarely confluent. Phycobiont a species of Chlorococcaceae, cells 5-8 µm diam.

Apothecia 0.25–0.45 mm diam. and 0.15 mm high, at first rounded, with a concave to plane, flesh coloured to light brown disc and a distinct, rather thick, slightly prominent, chamois-coloured margin, later often irregular in outline, with a slightly convex, dark reddish to purplish brown disc (very rarely with a thin, pale pruina), the margin soon disappearing. Exciple distinctly paraplectenchymatous, colourless, cells small, 3–5 μm diam. Hypothecium brown, 30–40 μm high; central apothecial base brown. Hymenium up to 50 μm high, colourless. Epithecium indistinct. Paraphyses 0.07 μm thick, branched and anastomosing. Asci clavate, 40–45 \times 8–12 μm , of the *Byssoloma* type. Ascospores 8 per ascus, 3-septate, oblong-ellipsoid, slightly constricted at the septa, colourless, 12–15(–17) \times 4–4.5 μm .

Pycnidia not seen.

Etymology: The name refers to the dispersed thallus, a rare feature in the genus.

Notes: This new species is readily distinguished by its discontinuous, dispersed, smooth, whitish green thallus, and its flesh-coloured to reddish or purplish brown apothecia. Up to the present, such a thallus morphology is known from *Fellhanera semecarpi* (with 1-septate ascospores and ochraceous brown apothecia), *F. pauciseptata* (see below), and *F. bullata* Kalb & Vezda (with strongly convex thallus patches and dark brown apothecia; Vezda & Kalb 1991).

Fellhanera dispersa is externally similar to *Loflammia gabrielis* (Müll. Arg.) Vezda (1986), which can be separated by the following anatomical details (Santesson 1952): exciple encrusted with colourless crystals, K+ yellow, then orange, hypothecium light brown, epithecium pale brown. Both species also seem to differ in their ecology, *F. dispersa* being more common at higher altitudes, whereas *Loflammia gabrielis* seems to prefer lowland sites. Their similarity is another hint for the possible relationships between *Fellhanera* and some genera with campylidia currently set apart in the Ectolechiaceae, e.g. *Barubria*, *Calopadia*, or *Tapellaria* (see Lücking et al. 1994).

Additional specimens examined: COSTA RICA. San José: Chirripó National Park, 9° 28' N, 83° 34' W, 1800–2200 m, primary upper montane rain forest,

92–303 (M). Las Quebradas, 9° 26' N, 83° 42' W, 1000–1100 m, primary and secondary montane rain forest, 92–4343 (hb. Lücking). Alajuela: Arenal Forest Reserve, 10° 28' N, 84° 40' W, 500 m, primary lower montane rain forest, 91–2164 (hb. Lücking). Limón: Braulio Carillo National Park, section Quebrada Gonzales, »Botarrama« trail, 10° 12' N, 83° 55' W, 480 m, forest margin, 91–310 (hb. Lücking).

Fellhanera elliotii (Vain.) Vezda (Fig. 3 C)

Specimens examined: COSTA RICA. Cartago: Cervantes, 9° 53' N, 83° 49' W, 1450 m, small relict forest, 91–3830 (hb. Lücking). Guayabo National Monument, 9° 59' N, 83° 43' W, 800–900 m, primary lower montane rain forest, 92–2018 (hb. Lücking).

Fellhanera emarginata R. Lücking sp.n. (Fig. 1 D–F, 6 A)

Fellhanera emarginata nom. nud. in Lücking, R., *Foliikole Flechten und ihre Mikrohabitatpräferenzen in einem tropischen Regenwald in Costa Rica*: 70 (1994); Lücking, R., *Bibl. Lichenol.* 58: 265 (1995).

Thallus epiphyllus, tenuissimus, continuous, laevigatus, cinereo-fuscus. Apothecia 0.15–0.25 mm diam., rotundata, convexa, fusca ad cinereo-fusca, emarginata. Excipulum indistinctum. Hypothecium obscure fuscum. Hymenium incoloratum. Paraphyses ramoso-connexae. Asci clavati, ad typum *Byssoloma* pertinentes. Ascospores 8-nae, 3-septatae, oblongo-ovales, 14–20 \times 4–5.5 μm . Alga ad Chlorococcaceas pertinens.

Typus: COSTA RICA. Limón: Braulio Carillo National Park, section Quebrada Gonzales, »Botarrama« trail, 10° 12' N, 83° 55' W, 480 m, primary submontane rain forest, on leaves of *Heliconia* sp., VII. 1991, leg. R. Lücking 91–5374 (ULM holotype).

Description: Thallus epiphyllous, thin, continuous, smooth, greyish brown, sometimes with a dark greenish grey marginal zone. Phycobiont a species of Chlorococcaceae, cells 4–9 μm diam.

Apothecia 0.15–0.25 mm diam. and 0.08–0.1 mm high, with a convex, brown to greyish brown disc, emarginate but with the marginal zone often slightly paler. Exciple much reduced, indistinct. Hypothecium brown, 15–20 μm high; central apothecial base not well distinguished in colour

from the surrounding tissue. Hymenium 45-50 µm high, colourless. Paraphyses 0.07 µm thick, branched and anastomosing. Asci clavate, 40-45 × 12-14 µm, of the *Byssoloma* type. Ascospores 8 per ascus, 3-septate, oblong-oval, with distinctly rounded ends, colourless, 14-20 × 4-5.5 µm.

Pycnidia not seen.

Etymology: The name refers to the emarginate apothecia.

Notes: *Fellhanera emarginata* is externally very similar to *F. angustispora*, and for some time I have hesitated to establish two separate taxa for this pair of species. However, the differences are constant, and no intermediate specimens were found. *F. emarginata* can be distinguished by its dark, usually brownish thallus, with the apothecia only indistinctly delimited in colour, and its constantly broader ascospores. Although in some cases, both species were found growing together on the same leaf, they appear to have different ecological preferences. Whereas *F. angustispora* is most common at lower altitudes (0-500 m), *F. emarginata* obviously prefers montane ranges (500-2000m).

Additional specimens examined: COSTARICA. San José: Braulio Carillo National Park, section La Hondura, 10° 02' N, 84° 00' W, 1500 m, primary montane rain forest and forest margin, 92-4769 (hb. Lücking). Cartago: Guayabo National Monument, 9° 59' N, 83° 43' W, 850-900m, secondary forest, 92-1558 (B), 92-1584 (UPS), 92-1641 (CR), 92-1798 (GZU), 92-1799 (ULM). Tapanti National Wildlife Refuge, »Oropendula« trail, 9° 46' N, 83° 46' W, 1200-1300m, primary montane rain forest, 91-3943 (hb. Lücking); *ibid.*, »La Pava« trail, 9° 46' N, 83° 47' W, 1500-1700m, primary montane to upper montane rain forest, 92-22 (hb. Lücking). Limón: Braulio Carillo National Park, section Quebrada Gonzales, »Botarrama« trail, 10° 12' N, 83° 55' W, 480 m, primary submontane rain forest, 91-1285 (hb. Lücking, with *F. angustispora*), 91-1286 (hb. Kalb), 91-1287 (STU), 91-1288 (BM), 91-1289 (M), 92-2521 (LG, NY).

A taxon closely related to *Fellhanera emarginata* was found in the montane forest belt [Cartago: Tapanti National Wildlife Refuge, 9° 46' N, 83° 47'

W, 1800m, forest margin at mirador, 91-3225, 91-3252 (hb. Lücking)]. The scanty specimens are externally similar to the latter but have narrower, 5-septate ascospores (Fig. 1 I).

Fellhanera fuscatula (Müll. Arg.) Vezda (Fig. 3 A-B)

Vezda, A., *Folia Geobot. Phytotax., Praha*, 21: 214 (1986). *Patellaria fuscatula* Müll. Arg., *Flora* 64: 231 (1881). Type: VENEZUELA. Caracas: Caracas, 1878, Ernst (G, lectotype!, here selected).

Patellaria fuscatula var. *nigricans* Müll. Arg., *Flora* 64: 231 (1881). Type: BRAZIL. São Paulo: Apiahy, 1879, Puiggarii 361 (G, holotype!).

Patellaria rufula Müll. Arg., *Flora* 64: 231 (1881). Type: BRAZIL. São Paulo: Apiahy, 1880, Puiggarii 1088 (G, lectotype!).

Lecidea mollissiaeformis Vain., *Journ. Bot.* 34: 101 (1896). Type: LESSER ANTILLES. St. Vincent: Bonhomme Woods, I. 1892, Elliott 351 (TUR, hb. Vainio 21661, holotype!).

Lecidea dominicana Vain., *Journ. Bot.* 34: 101 (1896). *Fellhanera dominicana* (Vain.) Vezda, *Folia Geobot. Phytotax., Praha*, 21: 214 (1986). Type: LESSER ANTILLES. Dominica: 1892, Elliott 517 (TUR, holotype!).

Lecidea scottii Vain., *Hedwigia* 37: 43 (1898). Type: UGANDA. Ruwenzori, 2700-2800m alt., 1893-94 Scott-Elliott 245 (TUR, holotype!).

Fellhanera farinosa nom. nud. in Lücking, *Beih. Nova Hedwigia* 104: 138 (1992).

Notes: Among the species of *Fellhanera* with brownish apothecia and greenish grey thalli, there are two closely related taxa separated by their 5-septate vs. 7-septate ascospores. The species with 5-septate ascospores was hitherto known as *F. fuscatula*, whereas the species with 7-septate ascospores was named *F. dominicana* (Santesson 1952; Vezda 1986; Lücking 1992a; Sérusiaux 1996). Both forms are widely distributed, but, as already noted by Sérusiaux (1996), the 5-septate taxon is much more abundant in tropical Africa and scarcely represented in tropical America, whereas the 7-septate form is most common in the Neotropics and rarely found in tropical Africa (Becker & Lücking 1995). Since both species are externally impossible to distinguish, their ascospores have to be carefully checked for sure identification, particularly since the formation of the final septa

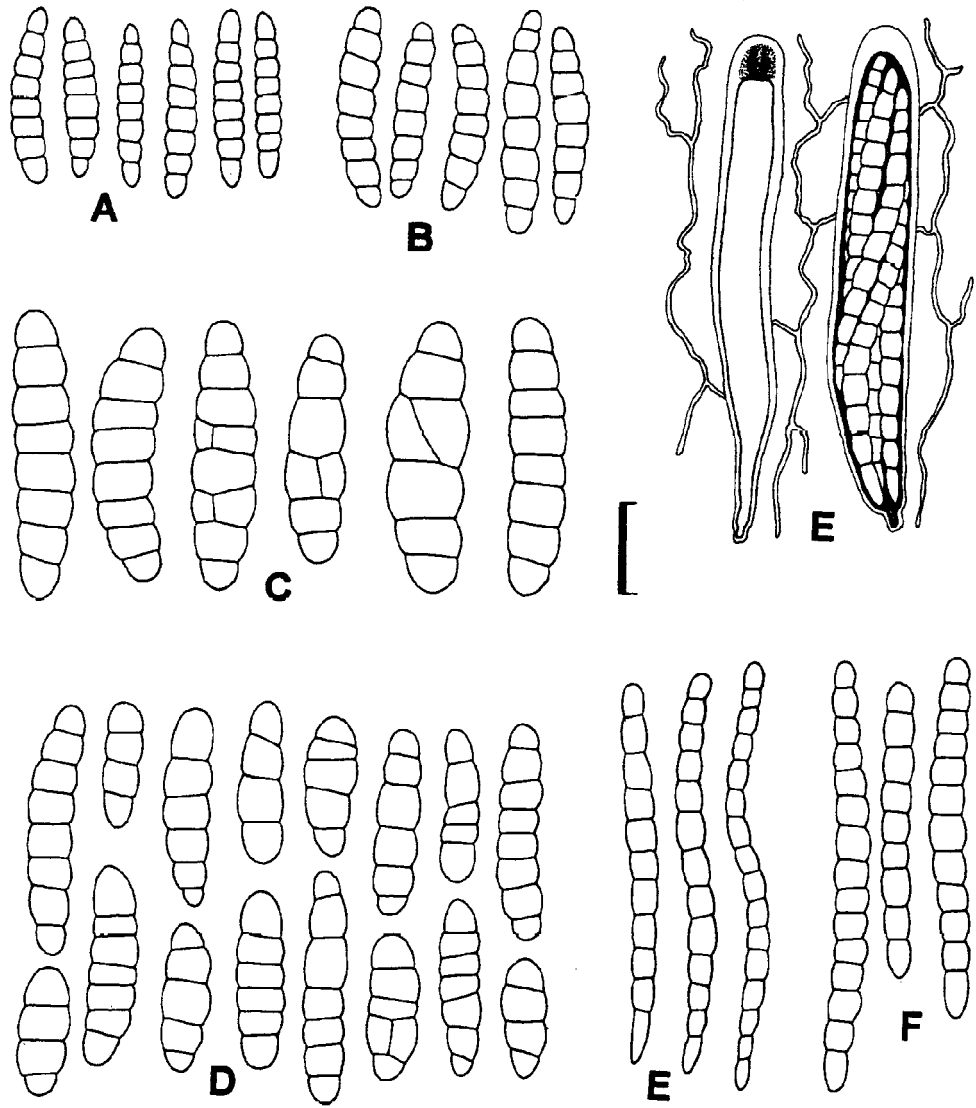


Figure 3. (A-B) *Fellhanera fuscata* [(A) 92-253, (B) 91-4113]. (C) *F. elliotii* [92-1500]. (D) *F. paradoxa* [91-2164]. (E-F) *F. longispora* [(E) 92-2014, (F) 91-4667]. Asci and ascospores. Scale = 10 μ m.

is often retarded. The situation is even more complicated if *Byssoloma fadenii* Vezda (1975) is taken into consideration, which has 5-7(-9)-septate ascospores and a much reduced byssoid exciple and is therefore easily mistaken for a *Fellhanera*. *Byssoloma fadenii* is known from tropical Africa and America; it has the same ecological preferences as the mentioned *Fellhanera* species and often occurs together with the latter on the same leaves.

Müller Argoviensis (1881) based his *Patellaria fuscatula* and two further taxonomic synonyms, viz. *P. fuscatula* var. *nigricans*, and *P. rufula*, all of which subsequently identified with the 5-septate taxon by Santesson (1952), on material from Venezuela and Brazil. Given the rareness of the typically 5-septate taxon in the Neotropics, it seemed rather strange to me that so many taxonomic synonyms should originate from the Neotropics. Therefore, with the difficulties as to correct evaluation of ascospore septation in mind, I studied the type material of the names in question. The type material of *Patellaria fuscatula* consists of four small leaf fragments. Two of them carry sterile thalli, and the other two have a few apothecia. One is a typical *Fellhanera*, with the ascospores badly developed but mostly 7-septate. The other specimen, with 5-7-septate ascospores, has a shortly byssoid exciple and is a rather depauperate *Byssoloma fadenii*. The *Fellhanera* was selected as lectotype of *Patellaria fuscatula*, which actually does not represent the typically 5-septate but the 7-septate taxon, hence providing an earlier name for the species hitherto known as *F. dominicana*.

The holotype of *Patellaria fuscatula* var. *nigricans* has rather dark apothecia damaged by water. The ascospores are predominantly 7-septate, as indicated on the label by Müller Argoviensis' notes and drawings. The lectotype of *Patellaria rufula* contains a mixture of several species, all badly developed, e.g. a *Porina* sp., a *Dimerella* sp., and a *Bapalmuia* sp. Again, the only *Fellhanera* apparent is one with mostly 7-septate, though rather broad ascospores. Pycnidia are also present, the conidia being simple, bacillar, c. 4×0.7 μm , representing the same type as described for African populations of the typically 5-septate species hitherto known as *F. fuscatula* (Sérusiaux 1996). It should be mentioned that also in the original descriptions of *Patellaria fuscatula*, its

var. *nigricans*, and *P. rufula* (Müller Argoviensis 1881), the ascospores are given as 5-6(-7)-septate.

Expecting that one of the two names published by Vainio and placed into synonymy of *Fellhanera fuscatula* by Santesson (1952) would then provide an epithet available for the taxon with 5-septate ascospores, I studied the corresponding types as well. However, the type material of *Lecidea mollissiaeformis* is a very typical representative of the form with 7-septate ascospores, and even the type of *Lecidea scottii*, although originating from tropical Africa, has predominantly 7-septate, rather broad ascospores.

The following material listed by Santesson (1952) among *Fellhanera* [= *Bacidia*] *fuscatula* was also studied: BRAZIL. Rio de Janeiro: Corcovado, 1889, Ule 24 (G): ascospores are 7-septate and as such illustrated by Müller Argoviensis on the label. BRAZIL. São Paulo: Apiahy, 1879-89, Puiggarii 1034, 1523, and s.n. (all in G): ascospores are 7-septate, as illustrated by Müller Argoviensis on some labels, e.g. in 1523. Two specimens from this locality, viz. 2321 and s.n. (both in G) belong to *Byssoloma fadenii*. Only one specimen from this collection (1883, s.n.) has the ascospores 5-septate. Also rather typical and provided with pycnidia is the following collection: PARAGUAY. Cordillera de Mbatobi, 1887, Balansa 4255. The conidia are bacillar to oblong, simple, and 4×1 μm . This material has been selected as type for *Fellhanera subfuscatula*, a new name established for the 5-septate form (see below).

The nomenclatural consequences of these findings are straightforward but most unfortunate since two common and well known taxa are involved, including the type species of *Fellhanera*. The names *F. fuscatula* and *F. dominicana* have to be synonymized, with *F. fuscatula* being the oldest name available for the taxon with 7-septate ascospores, up to the present known as *F. dominicana*. For the taxon hitherto named *F. fuscatula*, the new epithet *subfuscatula* is introduced below, based on a specimen originating from tropical America, but with purely 5-septate ascospores and pycnidia. When selecting *F. fuscatula* as the generic type, Vezda (1986) clearly referred to the typically 5-septate, mainly African taxon with which he was much more acquainted. With the new interpretation given here, the name *F. fuscatula* refers to the predominantly American

taxon with 7-septate ascospores. Systematically, this is a minor problem, since both taxa have identical morphological and anatomical features and the same pycnidia, and either of them could equally serve as generic type. On the other hand, the interpretative changes regarding the application of the epithets *fuscatula* and *dominicana*, and the necessary introduction of a further, new epithet, are most unfortunate, but I have seen no way to avoid them.

Fellhanera fuscatula, i.e. the 7-septate taxon, is extraordinarily variable. Its thallus is mostly smooth but may also be minutely farinose to granulose in certain situations, the colour varying from dark greenish or brownish grey to pale greenish grey. The apothecia are ochraceous yellow to dark brown, with an indistinct or well developed, pale margin. This variational amplitude is very similar to that found in the *Byssoloma leucoblepharum* aggregate, including *B. chlorinum* (Lücking 1995c). On the other hand, the anatomical features of *F. fuscatula* are rather constant, always having 7-septate ascospores, a brown hypothecium, and an aeruginous apothecial base. Given such a variation, I found it impossible to confirm the autonomous taxonomic status of the earlier proposed *F. farinosa* nom. nud., which represents one end of the extremes, viz. a pale greenish grey, farinose to granulose thallus and rather light apothecia with a distinct margin (Lücking 1992a). Such forms seem to be more frequent in open situations or at higher altitudes, whereas the lowland rain forest populations usually have a thin, dark thallus and darker apothecia.

Selected specimens examined: COSTA RICA. Guanacaste: Rincon de la Vieja National Park, »Santa Maria« to »Las Pailas« trail, 10° 45' N, 85° 18' W, 900-1000 m, primary lower montane moist forest, 92-124 (BM, GZU, M). Chirripó National Park, 9° 28' N, 83° 34' W, 1800-2200 m, primary upper montane rain forest, 92-253 (hb. Lücking); *ibid.*, 9° 28' N, 83° 33' W, 3000-3200 m, primary cloud forest below »Hopeless Mountain«, 92-548 (B, CR, GZU, LG, M, STU, UPS). Las Quebradas, 9° 26' N, 83° 42' W, 1000-1100 m, primary and secondary montane rain forest, 92-4336 (STU). Caño Negro National Wildlife Refuge, 10° 54' N, 84° 47' W, 50 m, isolated primary lowland rain forest, 92-2752 (CR, STU), 92-

2755 (M), 92-2756 (hb. Kalb), 92-2760 (NY), 92-3034 (UPS), 92-3071 (CBG). Heredia: La Selva Protection Zone, 10° 26' N, 84° 03' W, 50-100 m, swamp forest on SUA/CCC trails, 91-5370 (CR); *ibid.*, secondary forest on SOC trail, 91-5608 (VBI); *ibid.*, 50 m, primary and secondary forest around »Arboleda« trail, 91-1688 (B). Cartago: Alto La Gloria, Interamerican highway, 9° 48' N, 83° 57' W, 1700 m, gallery forest, 91-3606 (M). Guayabo National Monument, 9° 59' N, 83° 43' W, 850-900 m, secondary forest, 92-1401 (B), 92-1426 (STU), 92-1480 (hb. Kalb), 92-1601 (UPS), 92-1636 (STU). Puntarenas: Carara Biological Reserve, 9° 47' N, 84° 35' W, 50-100 m, primary lowland moist forest, 91-1818 (CR). Corcovado National Park, »Los Patos« to »Sirena« trail, 8° 31' N, 83° 34' W, 50-100 m, primary lowland rain forest, 92-3737 (LG); *ibid.*, »Sirena« to Rio Sirena trail, 8° 28' N, 83° 35' W, sea level, coastal lowland rain forest, 92-3280 (ULM). Las Mellizas, 8° 52' N, 82° 50' W, 1300 m, forest margin along road, 91-4104 (CR). Wilson's Botanical Gardens, 8° 48' N, 82° 57' W, 1000 m, primary lower montane rain forest, 91-4113 (hb. Lücking, filed under *F. longispora*). Limón: Braulio Carrillo National Park, section Quebrada Gonzales, »Botarrama« trail, 10° 12' N, 83° 55' W, 480 m, forest margin, 91-314 (BM), 91-315 (NY, hb. Lücking). Hitoy Cerere Biological Reserve, 9° 41' N, 83° 02' W, 100-200 m, primary lowland to submontane rain forest, 91-159 (UPS); *ibid.*, 100 m, primary lowland to submontane rain forest at the Rio Cerere, 91-4589 (BM), 91-4654 (UPS). Rio Corintho, 10° 12' N, 83° 53' W, 200 m, gallery forest along the Rio Corintho, 92-3849 (CR), 92-3940 (LG). Tortuguero National Park, 10° 32' N, 83° 30' W, sea level, primary lowland rain forest, 92-1832 (GZU); *ibid.*, Cerro Tortuguero, 10° 35' N, 83° 31' W, 0-100 m, primary lowland rain forest, 92-2683 (ULM); *ibid.*, 10° 32' N, 83° 30' W, sea level, *Citrus* and *Mangifera* trees in village, 92-1928 (NY).

Fellhanera lisowskii (Vezda) Vezda

Selected specimens examined: COSTA RICA. Alajuela: Caño Negro National Wildlife Refuge, 10° 54' N, 84° 47' W, 50 m, isolated primary lowland rain forest, 92-2763 (CBG). Heredia: La Selva Protection Zone, 10° 26' N, 84° 03' W, 50-100 m, primary lowland rain forest on CES/LOC/CEN trails, 91-4934 (hb. Lücking, filed under *F. badimioides*),

92-86 (hb. Lücking); *ibid.*, secondary forest on SOC trail, 91-5604 (CR, G, hb. Lücking). Puntarenas: Manuel Antonio National Park, 9° 22' N, 84° 09' W, 0-50 m, coastal lowland moist forest, 91-1284 (hb. Lücking). Limon: Braulio Carrillo National Park, section Quebrada Gonzales, »Botarrama« trail, 10° 12' N, 83° 55' W, 480 m, primary submontane rain forest, 91-1282 (hb. Lücking). Hitoy Cerere Biological Reserve, 9° 41' N, 83° 02' W, 100-200 m, primary lowland to submontane rain forest, 91-240 (ULM).

***Fellhanera longispora* R. Lücking** sp.n. (Fig. 3 E-F, 6 C)

Thallus epiphyllus, tenuis, continuus, laevigatus, viride cinereus. Apothecia 0.15-0.35 mm diam., rotundata, plana ad convexa, obscure fusca. Excipulum paraplectenchymaticum, incoloratum. Hypothecium rubro-fuscum ad obscure fuscum; pars basalis apothecii aeruginea. Hymenium incoloratum; epithecium pallide flavescens. Paraphyses ramoso-connexae. Asci clavati, ad typum *Byssoloma* pertinentes. Ascospores 8-nae, (7-)9-11-septatae, vermiformes, 30-35 × 4-4.5 μm. Alga ad Chlorococcaceas pertinens.

Typus: COSTARICA. Limon: Hitoy Cerere Biological Reserve, 9° 41' N, 83° 02' W, 100-200 m, primary lowland to submontane rain forest, on leaves of a dicotyledon, III. 1991, leg. R. Lücking 91-1306 (ULM holotype; G, NY, UPS, VBI, hb. Kalb, hb. Lücking isotypes).

Description: Thallus epiphyllous, thin, continuous, up to 25 mm across, smooth to very minutely farinose, pale greenish grey. Phycobiont a species of Chlorococcaceae, cells 5-9 μm diam.

Apothecia 0.15-0.35 mm diam. and 0.12-0.15 mm high, often numerous and then small but with a few larger ones peripheral on the same thallus, rounded, with a plane, dark brown disc and a thin, pale grey to chamois-coloured margin, rarely convex and with disappearing margin. Exciple distinctly paraplectenchymatous, colourless, up to 35 μm broad, cells 3-7 μm diam. Hypothecium dark brown to blackish brown, 25-35 μm high; central apothecial base aeruginous to blackish. Hymenium 55-70 μm high, colourless. Epithecium slightly yellowish. Paraphyses 0.05-0.07 μm thick, branched and anastomosing. Asci clavate, 50-60 × 8-10 μm, of the *Byssoloma* type. Ascospores 8

per ascus, (7-)9-11-septate, vermiform, colourless, 30-35 × 4-4.5 μm.

Pycnidia not seen.

Etymology: The epithet refers to the long, multi-septate ascospores.

Notes: This new species was first mentioned from El Salvador and Colombia by Nowak & Winkler (1970, 1972; see also Lücking 1992a) as an aberrant form of *Bacidia dominicana* [= *Fellhanera fuscata*]. The present material demonstrates an autonomous taxon close to *F. fuscata* (in the new interpretation given above), but differing by the constantly larger ascospores with more numerous septa: in *F. fuscata*, ascospores are (5-)7-septate and 18-27 μm long. *F. longispora* should not be confused with *F. paradoxa*, in which 9-septate ascospores may occur. The latter has lighter apothecia, and its ascospores are irregularly 3-9-septate or submuriform and much broader (4-7 μm).

The morphological amplitude of *Fellhanera longispora* is rather similar to that of *F. fuscata*, the thallus ranging from smooth to farinose, and the apothecia from having a distinct margin to almost emarginate. The lowland populations usually have a rather large, smooth thallus with numerous small but mature apothecia in the centre and some larger apothecia at the periphery. In populations originating from montane rain forest, the thallus is smaller and minutely farinose, and the apothecia are more homogeneous in size.

Additional specimens examined: COSTARICA. San José: Chirripó National Park, 9° 28' N, 83° 34' W, 1800-2200 m, primary upper montane rain forest, 92-325 (hb. Lücking). Heredia: La Selva Protection Zone, 10° 26' N, 84° 03' W, 50-100 m, secondary forest on SOC trail, 91-5668 (hb. Lücking). Cartago: Centro Agronómico Tropical de Investigación y Enseñanza (C.A.T.I.E.), section Florencia, 9° 53' N, 83° 41' W, 700-750 m, secondary forest, 91-3675 (CR). Guayabo National Monument, 9° 59' N, 83° 43' W, 800-900 m, primary lower montane rain forest, 92-2014 (hb. Lücking). Puntarenas: Carara Biological Reserve, 9° 47' N, 84° 35' W, 50-100 m, primary lowland moist forest, 91-1819 (hb. Lücking). Limon: Hitoy Cerere Biological Reserve, 9° 41' N, 83° 02' W, 100 m, primary lowland to submontane

rain forest at the Rio Cerere, 91-4667 (hb. Lücking). Wilson's Botanical Gardens, 8° 48' N, 82° 57' W, 1000 m, primary lower montane rain forest, 91-4113 (hb. Lücking, with *F. fuscatula*).

**Fellhanera misionensis* Ferraro & R. Lücking ined.

Notes: *Fellhanera misionensis* is a new species to be described from Argentina (Ferraro & Lücking, in prep.). It is close to the African *F. vandenberghenii* (Sérus.) Vezda, having similar thallus, dark apothecia, and 1-septate ascospores, but differing in the larger apothecia (up to 0.7 mm diam.), the yellowish hypothecium, and the larger ascospores (up to 16 µm long). Since the most characteristic feature of *F. vandenberghenii* are the beaked pycnidia (Sérusiaux 1983), the persistent absence of pycnidia is taken as an additional argument to describe the neotropical populations as a new species, although this is a negative character, and the taxonomic validity of *F. misionensis* is pending until pycnidia of any type are discovered.

Selected specimens examined: COSTA RICA. San José: Braulio Carrillo National Park, section La Hondura, 10° 02' N, 84° 00' W, 1500 m, primary montane rain forest and forest margin, 92-4763 (hb. Lücking). Chirripó National Park, 9° 28' N, 83° 32' W, 2550-2800 m, primary cloud forest, 92-444 (hb. Lücking). Cartago: Tapanti National Wildlife Refuge, »La Pava« trail, 9° 46' N, 83° 47' W, 1500-1700 m, primary montane to upper montane rain forest, 92-25 (LG, hb. Lücking). Birrisito, 9° 49' N, 83° 50' W, 1200 m, *Citrus* and *Mangifera* trees and coffee plantations along road, 91-2793 (hb. Lücking).

Fellhanera montana R. Lücking sp.n. (Fig. 2A, 5C)

Thallus epiphyllus, tenuis, continuus, farinosus, viride ad flavo-cinereus. Apothecia 0.3-0.5 mm diam., rotundata, basi constricta; discus fuscus, margo concolor vel pallidior. Excipulum parte basali paraplectenchymaticum, incoloratum. Hypothecium fuscum; pars basalis apothecii nigro-aeruginea. Hymenium incoloratum; epithecium pallide flavido-fuscum. Paraphyses ramoso-connexae; asci clavati, ad typum *Byssoloma* pertinentes. Ascospores 8-nae, muriformes, ellip-

soideae ad ovoideae, 30-38 × 12-16 µm. Alga ad Chlorococcaceas pertinens.

Typus: COSTA RICA. San José: Braulio Carrillo National Park, section La Hondura, 10° 02' N, 84° 00' W, 1500 m, primary montane rain forest and forest margin, on leaves of a dicotyledon, I. 1992, leg. R. Lücking 92-4762 (ULM holotype).

Description: Thallus epiphyllous, thin, continuous, irregularly in outline, farinose, greenish to yellowish grey. Phycobiont a species of Chlorococcaceae, cells 5-9 µm diam.

Apothecia 0.3-0.5 mm diam. and 0.17-0.2 mm high, with a plane, dark purplish brown disc and a margin of similar or slightly paler colour. Exciple basally paraplectenchymatous, colourless, laterally composed of narrow, thick-walled, somewhat curved cells giving a labyrinthical appearance, up to 35 µm broad. Hypothecium brown, 20-35 µm high; central apothecial base blackish, with a slight aeruginous tinge. Hymenium 95-110 µm high, colourless. Epithecium slightly yellowish brown. Paraphyses 0.07 µm thick, richly branched and anastomosing. Asci clavate, 90-100 × 24-28 µm, of the *Byssoloma* type (often difficult to see). Ascospores 8 per ascus, muriform, with 5-7 transverse and 1-3 longitudinal septa, ellipsoid to ovoid, colourless, 30-38 × 12-16 µm.

Pycnidia not seen.

Etymology: The name refers to the fact that the two localities at which the species was found are confined to the (upper) montane forest belt.

Notes: This new species is distinguished from all other members of the genus by the eight, distinctly muriform ascospores per ascus (not submuriform as in *Fellhanera paradoxa* or *F. elliottii*). Its general appearance, together with the ascospore type, seem to place *F. montana* in a continuous series of species with transversely septate to muriform ascospores, providing a connection between *F. elliottii* and *F. dictyospora*. However, the excipular structure of *F. montana* deviates slightly from the other species (including *F. dictyospora*), the cells having thicker walls and very narrow, partly elongate and curved lumina (Fig. 5C).

Additional specimens examined: San José: Chirripó National Park, 9° 28' N, 83° 33' W, 3000-3200 m, primary cloud forest below »Hopeless Mountain«, 92-544 (hb. Lücking).

Fellhanera muhleii R. Lücking sp.n. (Fig. 6 D-E)

Thallus epiphyllus, tenuissimus, continuus, laevigatus, viride cinereus ad cinereo-fuscus, sorediis pallide cinereo- ad flavo- viridibus instructus. Apothecia 0.25-0.4 mm diam., cinereo-nigra ad fusca, pruinosa. Excipulum paraplectenchymaticum, incoloratum. Hypothecium fuscum; pars basalis apothecii aeruginea. Hymenium incoloratum; epithecium pallide flavum ad viride fuscum. Paraphyses leviter ramoso-connexae. Asci clavati, ad typum *Byssoloma* pertinentes. Ascosporae 2-4(-8)-nae, 3-septatae, oblongo-ellipsoideae, 15-20 × 4-4.5 µm. Alga ad Chlorococcaceas pertinens.

Typus: COSTA RICA. Heredia: La Selva Protection Zone, 10° 26' N, 84° 03' W, 50 m, forest margin on SHO trail, on leaves of a dicotyledon, IX. 1991, leg. R. Lücking 91-4775 (ULM holotype; hb. Lücking isotype).

Description: Thallus epiphyllous, thin, continuous, patches often confluent and covering large areas of the phorophyte leaf, smooth, greenish grey to greyish or reddish brown, provided with pale greyish to yellowish green soralia which usually form a sharp contrast with the thallus surface. Soralia at first visible as small points (0.05-0.1 mm) at the thallus margin, later up to 0.3 mm in diam. and rounded but eventually becoming confluent and covering large areas of the thallus, rarely the whole thallus dissolved into an effuse soredial mass. Soredia when young 9-12 µm diam., with one rather large algal cell (5-8 µm), later up to 20 µm diam. and with several smaller (3-4 µm) ones, wrapped up with rather thin, colourless hyphae. Phycobiont a species of Chlorococcaceae, cells 5-8 µm diam.

Apotheciarare, 0.25-0.4 mm diam. and 0.12-0.15 mm high, at first rounded, with a concave, greyish black disc provided with whitish pruina, and with a distinct, slightly prominent, whitish margin, later often somewhat irregular in outline, with a plane to strongly convex, dark brown disc provided with a pale yellowish pruina, and with the margin becoming greyish and disappearing. Exciple distinctly paraplectenchymatous,

colourless, cells 3-7 µm diam. Hypothecium rather dark brown, 35-50 µm high; central apothecial base aeruginous. Hymenium up to 50 µm high, colourless to pale yellowish. Epithecium yellowish to greenish brown. Paraphyses 0.07-1 µm thick, slightly branched and anastomosing. Asci clavate, 40-45 × 8-12 µm, of the *Byssoloma* type. Ascospores 2-4(-8) per ascus (some ascospores often degenerated), 3-septate, oblong-ellipsoid, colourless, 15-20 × 4-4.5 µm.

Pycnidia not seen.

Etymology: *Fellhanera muhleii* is dedicated to Dr. Hermann Muhle, a distinguished colleague who very much stimulated my initial work on foliicolous lichens.

Notes: *Fellhanera muhleii* is easily recognized by its sorediate thallus and its rather dark, pruinose apothecia with usually 2-4, 3-septate ascospores per ascus. This characteristic new species seems to be most closely related to *F. santessonii* (Barillas & Lücking 1992), which has very similar apothecia but a rather indistinct thallus without soralia and regularly 8-spored asci. From other species with soralia, viz. *F. seroexpectata* Sérus., *F. viridis* (see below), *F. sorediantha* (Vezda) Vezda, and *F. lambinonii* (Sérus.) R. Lücking & Sérus., *F. muhleii* is mainly distinguished by the blackish, pruinose apothecia, in combination with the thin thallus and the yellowish green soralia.

Additional specimens examined: COSTA RICA. Alajuela: Caño Negro National Wildlife Refuge, 10° 54' N, 84° 47' W, 50 m, isolated primary lowland rain forest, 92-2754 (hb. Lücking). Heredia: La Selva Protection Zone, 10° 26' N, 84° 03' W, 50-100 m, secondary forest on SUR trail, 91-1983 (CR, hb. Lücking). Cartago: Alto La Gloria, Interamerican highway, 9° 48' N, 83° 57' W, 1700 m, gallery forest, 91-3620 (hb. Lücking). Puntarenas: Rio Rincon, 8° 36' N, 83° 31' W, 50 m, primary lowland rain forest along the Rio Rincon, 92-3428 (hb. Lücking).

Fellhanera paradoxa (Vezda) Vezda

Notes: *Fellhanera paradoxa* is very closely related to *F. elliottii*, and the two species are often difficult to separate. According to my observations, ascospores in the latter are usually 7-septa-

te as in *F. fuscata* but much broader, and some longitudinal septa are present. The number of ascospores per ascus is mostly eight. In *F. paradoxa*, the ascospores may be similar in part, but here, the ascospores are generally very irregular in size and septation, with small 3-septate and large submuriform ascospores occurring in the same hymenium or even in the same asci. Accordingly, the number of ascospores per ascus may vary between two and eight.

Specimens examined: COSTA RICA. Cartago: Guayabo National Monument, 9° 59' N, 83° 43' W, 800-900 m, primary lower montane rain forest, 92-2164, 92-2256 (both hb. Lücking); *ibid.*, 850-900 m, secondary forest, 92-1500 (hb. Lücking).

Fellhanera pilomarginata R. Lücking sp.n. (Fig. 5 A-B, 6 G-H)

Fellhanera fusciorubra nom. nud. in Lücking, R., *Foliikole Flechten und ihre Mikrohabitatpräferenzen in einem tropischen Regenwald in Costa Rica*: 70 (1994); Lücking, R., *Bibl. Lichenol.* 58: 265 (1995).

Thallus epiphyllus, tenuissimus, continuus, laevigatus, flavescenter ad viride cinereus. Apothecia 0.2-0.4(-0.5) mm diam., plana ad convexa, fusco-rubra, margine distincto instructa. Excipulum parte interno paraplectenchymaticum, parte externo byssoideum, incoloratum. Hypothecium flavescenter fuscum; pars basalis apothecii fuscescens. Hymenium incoloratum. Paraphyses leviter ramoso-connexae. Asci clavati, ad typum *Byssoloma* pertinentes. Ascospores 8-nae, 3-septatae, oblongae ad bacillares, 12-15 × 2.5-3 µm. Pycnidia frequentia, parte basali usque ad 0.05 mm lata, paraplectenchymatica, pallide flavido-fusca, parte apicali strato conidiogeno provisa. Celulae conidiogenae simplices, 15-20 × 1 µm. Conidia anguste clavata ad oblongo-ellipsoidea, 3-4 × 1 µm. Alga ad Chlorococcaceas pertinens.

Typus: COSTA RICA. Limon: Braulio Carillo National Park, section Quebrada Gonzales, »Botarrama« trail, 10° 12' N, 83° 55' W, 480 m, primary submontane rain forest, on leaves of *Chamaedorea tepejilote*, VII 1992, leg. R. Lücking 92-5100 (ULM holotype; hb. Lücking isotype).

Description: Thallus epiphyllous, thin, continuous, irregular in outline, smooth, pale yellowish to

greenish grey. Phycobiont a species of Chlorococcaceae, cells 5-9 µm diam.

Apothecia 0.2-0.4(-0.5) mm diam. and 0.12-0.15 mm high, rounded, but later irregularly incised to lobate; disc at first plane, soon convex, with a matt, reddish brown disc and a always distinct, whitish to chamois-coloured margin; the surface of the margin very minutely pilose (high magnification!). Exciple in its inner parts paraplectenchymatous, pale yellowish, c. 10 µm thick, in its outer parts (15-20 µm) consisting of short, loosely woven, uncoloured hyphae. Hypothecium yellowish brown, with a distinct yellowish zone above, 20-30 µm high; central apothecial base brownish. Hymenium up to 50 µm high, colourless. Paraphyses 0.07 µm thick, slightly branched and anastomosing. Asci clavate, 40-45 × 8-10 µm, of the *Byssoloma* type. Ascospores 8 per ascus, 3-septate, oblong to bacillar, colourless, 12-15 × 2.5-3 µm.

Pycnidia frequent, especially on thalli lacking apothecia, up to 0.1 mm high, with a basal, up to 0.05 mm broad socle consisting of a pale yellowish brown, paraplectenchymatous tissue. Upper part concave, exposing the colourless, conidiogeneous layer. Conidiogeneous cells 15-20 × 1 µm. Conidia narrowly pyriform to oblong-ellipsoid, 3-4 × 1 µm.

Etymology: The chosen epithet refers to the slightly hairy apothecial margin. Originally, I intended to describe the species with the epithet *fusciorubra*, because of its conspicuous, reddish brown apothecia, and this epithet has been spread in two papers. However, E. Sérusiaux (pers. comm. 1997) has directed my attention to the fact that this epithet might cause confusion with *Barubria fusciorubra* (Vezda) Vezda, a species with campylidia which, on account of its apothecia and thallus structure, bears great similarities with the genus *Fellhanera*.

Notes: This characteristic new species has two distinctive traits: the excipular structure, with the inner parts paraplectenchymatous and the outer parts byssoid, and the peculiar, apically widely open pycnidia. A similar exciple is found in *Byssoloma syzygii* Vezda & Vivant (Vezda 1994), but in that species, it is encrusted with crystals, and the apothecia are darker and the ascospores

larger and provided with more numerous septa. The widely open pycnidia of *Fellhanera pilomarginata* are rather unique among the Pilocarpaceae. In species of *Fellhanera*, e.g. *F. bouteillei* or *F. sublecanorina*, and *Byssoloma*, the pycnidial ostiole is often rather wide, but the conidiogenous layer is not fully exposed. In fact, the pycnidia of *Fellhanera pilomarginata* resemble sporodochia rather than genuine pycnidia, although they are probably derived from “normal” pycnidia. In some way they resemble the pycnidia of *Fellhaneropsis* (Sérusiaux 1996), but their anatomy is quite different. The conidia themselves are intermediate between the two types known in *Fellhanera* (oblong-bacillar to fusiform or pyriform) and *Byssoloma* (pyriform).

Although the excipular structure of *Fellhanera pilomarginata* is also intermediate between *Fellhanera* and *Byssoloma*, and an ally is eventually found in *Byssoloma syzygii*, the new species has provisionally been assigned to *Fellhanera*, as is the case with the two species with reduced exciple described above, *F. angustispora* and *F. emarginata*. This decision is based on the following arguments: Character variation within a given taxon is a reflexion of its evolutionary potential. Variation of characters of higher taxonomic value in the Pilocarpaceae is mainly found in the excipular structure and the conidiomata, as exemplified by the circumscription of *Fellhanera*, *Byssoloma*, *Byssolecania*, and *Badimia* (Vezda 1986; Lücking et al. 1994), and the recent description of *Fellhaneropsis* (Sérusiaux 1996). However, the ancestor of the Pilocarpaceae must have had a single type of exciple and conidiomata. It could be suspected that the exciple of such an ancestral taxon was prosoplectenchymatous, a rather primitive, widely distributed type of fungal tissue quite intermediate between the great variety of excipular types now found in the Pilocarpaceae. In that case, both the paraplectenchymatous exciple of *Fellhanera* and the byssoid type of *Byssoloma* would be apomorphic, and the placement of species like *Fellhanera pilomarginata* or *Byssoloma syzygii*, with a combination of two different apomorphic states in the same character, would be rather ambiguous. However, it could also be argued that the paraplectenchymatous exciple characteristic of *Fellhanera* represents the most plesiomorphic state, from which the other types

evolved through reduction and modification (Lücking et al. 1994). In some species of *Fellhanera*, there is a tendency to deposit crystals in the exciple, and this usually leads to a loosening of the excipular tissue and the formation of free hyphae at the apothecial margins, as seen in *F. stanhopeae* or species of *Badimia*.

No matter whether *Fellhanera* or another, perhaps hypothetical, genus is considered to be basic to the Pilocarpaceae, such a taxon must already carry the evolutionary potential causing the subsequent generic diversification in the family. It must then be assumed that similar apomorphic character states, such as a byssoid or reduced exciple, could have evolved independently from the ancestral taxon. This means that the generic placement of species not sharing a clear synapomorphy is doubtful. Even the byssoid exciple of *Byssoloma* is not necessarily an unambiguous synapomorphy (Lücking et al. 1994), although most species of *Byssoloma* are closely related to each other and exhibit rather uniform conidiomata. Therefore, any species which does not share the typical *Byssoloma* type exciple but merely a tendency towards that character could have evolved independently from the more basic genus, e.g. *Fellhanera*. Such a species can either be included in the genus characterized by the apomorphic or in the taxon having the plesiomorphic character state, or it is accommodated in a separate entity. Inclusion in the apomorphic genus would eventually produce a polyphyletic, unnatural taxon, since the possibility of independent evolution cannot be excluded, while inclusion in the plesiomorphic genus would create a more broadly defined but still natural taxon. The latter option has therefore been convincingly erected as a taxonomic principle in such cases (Cronquist 1988). The alternative solution, i.e. the consequent description of new genera based on species with imperfectly developed apomorphies, would eventually lead to a great number of small or monotypic entities representing evolutionary dead ends and hence obstructing the aims of higher taxonomy.

The three possibilities outlined above have been carefully considered for the species in question, *Fellhanera angustispora*, *F. emarginata*, and *F. pilomarginata*. The first option, the inclusion in the supposedly apomorphic genus

Byssoloma, has been rejected, since the excipular types found in these species are not completely identical with the latter, and their is a high probability of parallel evolution. Its not even clear whether *Fellhanera pilomarginata*, with its peculiar pycnidia, is actually related to *Byssoloma syzygii*, although both have a similar excipular type. New genera for this and the other two species have not been erected because, with the present knowledge, they might represent single apomorphic taxa rather than well distinguished groups of species deserving generic rank. Furthermore, our knowledge of non-foliicolous taxa to be included in the Pilocarpaceae is not yet settled, and there might exist genera or generic names which could serve to accomodate such species. I won't exclude the possibility that, with additional data, new genera will be described for the above taxa in the future, but for the time being, I have adopted the most conservative solution, their inclusion in the genus which supposedly exhibits the plesiomorphic character state, i.e. *Fellhanera*.

***Fellhanera rhapsidophylli* (Rehm) Vezda**

(?)*Fellhanera pilosa* nom. nud. in Lücking, R., *Beih. Nova Hedwigia* 104: 136 (1992).

Notes: *Fellhanera rhapsidophylli* belongs to a group of species, including *F. subternella* and *F. subfuscatula*, whose taxonomic status and range of variability in the Neotropics is difficult to establish, due to the scanty, heterogeneous, often badly developed collections. The types of *F. rhapsidophylli* (= *Bilimbia rhapsidophylli* Rehm; S, holotype) and of its taxonomic synonym, *Bilimbia caryotae* Vain. (TUR, holotype), both from the Philippines, have been carefully examined. Both originate from almost the same locality and a similar phorophyte and represent exactly the same morphological state. The thallus is finely farinose, and the apothecia are plane to slightly convex, with a thin margin, their colour varying from light to dark brown. The hypothecium is (pale to) rather dark brown, and the apothecial base aeruginous. All the collections cited below agree well with these features. The morphological and anatomical variation of *F. rhapsidophylli* is the same as found in the closely related *F. subfuscatula* (ascospores 5-septate) and *F. fuscatula* (ascospores 7-septate).

In an earlier treatment of the foliicolous lichens of Costa Rica (Lücking 1992a), two further, invalid names were listed. The specimen named *Fellhanera tuckeri* Vezda nom. nud. belongs to *F. rhapsidophylli*. It has been identified with a different name since at that time, the abundant material now described as a new species, *F. emarginata*, was assigned by me to *F. rhapsidophylli*. The other name, *F. pilosa* nom. nud., could not be confirmed by additional material. The thallus hairs on the only available specimen are a doubtful character and might be caused by uncoordinated fungal outgrowth, but even without these hairs, the material does not match any other species perfectly, although it is very close to *F. rhapsidophylli*. A further collection, identified as *F. buxi* Vezda & Vivant (Lücking (1992a), now considered as a synonym of *Fellhaneropsis myrtillicola* (Sérusiaux 1996), does not belong to that species (E. Sérusiaux, pers. comm. 1995). Its taxonomic status remains open until more material has been found. Thus, together with *F. farinosa* nom. nud., the names *F. tuckeri* nom. nud., *F. pilosa* nom. nud. and *F. buxi*, have to be deleted from the foliicolous lichen flora of Costa Rica.

Selected specimens examined: COSTA RICA. San José: Chirripó National Park, 9° 28' N, 83° 34' W, 1800-2200m, primary upper montane rain forest, 92-323 (hb. Lücking). Heredia: La Selva Protection Zone, 10° 26' N, 84° 03' W, 50-100 m, secondary forest on SUR trail, 91-1999 (hb. Lücking). Puntarenas: Manuel Antonio National Park, 9° 22' N, 84° 09' W, 0-50 m, coastal lowland moist forest, 91-411 (hb. Lücking). PHILIPPINES. Luzon: Bulucan, Baliung, 1910, Robinson 9641 (TUR holotype of *Bilimbia caryotae*). Laguna Los Baños, 1913, Raimundo comm. Baker 1817 b (S holotype of *Bilimbia rhapsidophylli*).

Incorrect records: The specimens cited as *Fellhanera rhapsidophylli* in Lücking (1992a) belong to *F. emarginata*.

Key to the species of *Fellhanera* and related or similar taxa known from Costa Rica with brownish apothecia and 3-septate ascospores

The Costa Rican material which falls into a broad concept of *Fellhanera rhapsidophylli* can be divided into several species which, by careful exami-

nation, are reasonably well distinguished from each other: *F. rhapsidophylli* s.str., *F. rubida* (see below), *F. angustispora*, and *F. emarginata*. These species might further be confused with *F. pilomarginata*, *Byssoloma* spp., and *Barubria fuscorubra*. Particularly the latter is almost impossible to distinguish from *Fellhanera* when campylidia are absent. In order to facilitate separation of these taxa, a key to the species or species groups known from Costa Rica is presented here:

1a Exciple reduced or absent, its structure shortly byssoid or indeterminable; apothecia appearing emarginate

2a Exciple shortly byssoid; apothecia often irregularly incised, ochraceous yellow or (light) reddish brown

see *Byssoloma minutissimum* Kalb & Vezda, *B. aurantiacum* Kalb & Vezda

2b Exciple completely reduced; apothecia mostly regularly rounded, dark brown

3a Thallus usually dark brownish grey, apothecia hardly contrasting in colour; ascospores $14-20 \times 4-5.5 \mu\text{m}$ *Fellhanera emarginata*

3b Thallus pale greenish grey, apothecia sharply contrasting in colour; ascospores $10-16 \times 2-3 \mu\text{m}$ *Fellhanera angustispora*

1b Exciple well developed, at least the inner parts distinctly paraplectenchymatous; apothecia with a more or less distinct margin

4a Lateral part of the exciple shortly byssoid; apothecial margin very distinct, chamois-coloured; pycnidia, if present, widely open, with the conidial mass exposed

Fellhanera pilomarginata

4b Exciple in all parts distinctly paraplectenchymatous; apothecial margin usually not sharply delimited; pycnidia, different from above, or bluish grey campylidia present

5a Thallus granulose to minutely effuse-arachnoid, usually with bluish grey campylidia producing simple or 1-septate, clavate conidia; apothecia rat-

her light orange brown; hypothecium pale yellowish brown, exciple small-celled (cells $3-7 \mu\text{m}$ in diam)

Barubria fuscorubra

5b Thallus smooth to farinose or granulose, campylidia absent; hypothecium yellowish brown to dark brown, if pale, then exciple large-celled ($8-15 \times 4-6 \mu\text{m}$)

6a Apothecia orange brown; exciple large-celled (especially basally), cells $8-15 \times 4-6 \mu\text{m}$; hypothecium light yellowish brown; central apothecial base yellowish brown *Fellhanera rubida*

6b Apothecia light to dark brown; exciple small-celled ($3-7 \mu\text{m}$); hypothecium light to dark brown; central apothecial base aeruginous

Fellhanera rhapsidophylli

Fellhanera rubida (Müll. Arg.) R. Lücking comb.n.

Patellaria rubida Müll. Arg., *Lichenes Epiphylli* Novi: 6 (1890). Type: BRAZIL. São Paulo: Apiahy, Puiggari s.n. (G holotype!).

Notes: *Patellaria rubida* was considered as a synonym of *Bacidia* (= *Fellhanera subternella*) by Santesson (1952), although said to have a different apothecial colour. The type material was examined and found to match specimens of the *Fellhanera rhapsidophylli* aggregate with orange brown apothecia and a large-celled exciple (see key below *F. rhapsidophylli*). The new combination *F. rubida* is therefore taken up. Although externally similar to *F. rhapsidophylli*, *F. rubida* is indeed close to *F. subternella*, differing in the pale greenish instead of bluish thallus and the brownish instead of yellowish apothecia. Both agree in the very large excipular cells and the yellowish brown apothecial base. Because of the different thallus

colour, it is expected that *F. rubida* and *F. subternella* differ in their secondary chemistry, but the material available so far has not allowed a thorough study of both taxa in this respect. Given that such differences exist, it cannot be quite excluded that *F. rubida* represents a chemical race of *F. subternella* (or viceversa), and its reinstatement should stimulate further studies on this question.

Selected specimens examined: COSTA RICA. Heredia: La Selva Protection Zone, 10° 26' N, 84° 03' W, 50-100 m, primary lowland rain forest on CES/LOC/CEN trails, 91-5203 (hb. Lücking); *ibid.*, 50 m, *Citrus* trees near administration building, 91-4883 (hb. Lücking). Cartago: Birrisito, 9° 49' N, 83° 50' W, 1200 m, *Citrus* and *Mangifera* trees, and coffee plantations along road, 91-2793 (hb. Lücking). Puntarenas: Corcovado National Park, »Los Patos«, 8° 34' N, 83° 31' W, 50-150 m, primary lowland rain forest, 92-3115 (hb. Lücking).

Fellhanera santessonii Barillas & R. Lücking

Selected specimens examined: San José: Braulio Carrillo National Park, former section Carillo, »Botella« trail, 10° 09' N, 83° 58' W, 750 m, primary lower montane rain forest, 91-3147 (STU). Chirripó National Park, 9° 28' N, 83° 34' W, 1800-2200 m, primary upper montane rain forest, 92-250 (hb. Lücking); *ibid.*, 9° 28' N, 83° 33' W, 2200-2550 m, primary upper montane rain forest, 92-365 (UPS). Alajuela: Arenal Forest Reserve, 10° 28' N, 84° 40' W, 500 m, primary lower montane rain forest, 91-2072 (CR, GZU, LG, M, hb. Kalb, hb. Lücking). Heredia: La Selva Protection Zone, 10° 26' N, 84° 03' W, 50-100 m, primary lowland rain forest on CES/LOC/CEN trails, 91-4924 (NY). Cartago: Alto La Gloria, Interamerican highway, 9° 48' N, 83° 57' W, 1700 m, gallery forest, 91-3607 (B). Guayabo National Monument, 9° 59' N, 83° 43' W, 850-900 m, secondary forest, 92-1635 (hb. Lücking). Limón: Braulio Carrillo National Park, section Quebrada Gonzales, »Botarrama« trail, 10° 12' N, 83° 55' W, 480 m, primary submontane rain forest, 91-4703 (VBI), 92-1989 (ULM), 92-5575 (hb. Lücking).

Fellhanera semecarpi (Vain.) Vezda

Notes: *Fellhanera semecarpi* was described as an

inconspicuous species with small apothecia (Santesson 1952). Most of the present material confirms this view, but some few specimens have been found in which the thallus is rather well developed and the apothecia are up to 0.4 mm large. Since the smaller apothecia of these thalli agree perfectly with the description given by Santesson, there seems to be no reason to separate these specimens as an autonomous taxon. There is also a certain variability concerning the colour of the apothecial disc, which ranges from ochraceous yellow or light yellowish brown to reddish or even dark brown (different colours can be found on apothecia of the same thallus). *F. semecarpi* is obviously a rare species which, however, can be locally common. At one site (»Botarrama« trail), it has been found abundantly in the understory, in the canopy, and at the forest margin, mostly on leaves not colonized by other lichens, indicating that this species is a weak competitor.

Well developed specimens of *Fellhanera semecarpi* come close externally to a species described as *Bacidia pauciseptata* by Santesson (1952). Examination of the type material of the latter revealed that it is a typical *Fellhanera*, making the following combination necessary: *Fellhanera pauciseptata* (R. Sant.) R. Lücking comb.n. [Bas.: *Bacidia pauciseptata* R. Sant., Symb. Bot. Ups. 12: 476 (1952). Type: COLOMBIA. Cauca, at El Tambo, 1700 m, 1938, von Sneidern s.n. (S holotype!)]. *Fellhanera pauciseptata* differs from *F. semecarpi* mainly by its ascospores, which in the type material are irregularly 1-3-septate. Most of the ascospores give the impression of still immature ones, indicating that the actual number of ascospore septa might be three (especially as the 2-septate ascospores have the distal cell about twice as large as the two proximal cells).

Selected specimens examined: San José: Chirripó National Park, 9° 28' N, 83° 34' W, 1800-2200 m, primary upper montane rain forest, 92-246 (hb. Lücking). Limón: Braulio Carrillo National Park, section Quebrada Gonzales, »Botarrama« trail, 10° 12' N, 83° 55' W, 480 m, primary submontane rain forest, 91-1277 (hb. Kalb), 91-1278 (B, UPS), 91-1298 (BM, CR, GZU, LG, M, NY, STU, hb. Lücking); *ibid.*, forest margin, 92-1999 (hb. Lücking, with *F. bouteillei*). Cahuita National Park, section Kelly Creek, 9° 44' N, 82° 50' W, sea level, coastal lowland

rain forest, 92-4143 (hb. Lücking).

***Fellhanera stanhopeae* (Müll. Arg.) R. Lücking, Lumbsch & Elix**

Lücking, R., Lumbsch, H. T. & Elix, J. A., *Bot. Acta* 107: 400 (1994). *Badimia stanhopeae* (Müll. Arg.) Vezda, Lich. Sel. Exs., Brno, Fasc. XCIII: 2 (1989).

Notes: *Fellhanera stanhopeae* is found in two different morphs. Typical specimens have a coarsely but very regularly verrucose thallus and numerous apothecia. This form is rather frequent in closed forests at low elevations. The other form consists of mostly sterile thalli, in which the thallus verrucae frequently break up into soralia. These thalli may cover large areas of the phorophyte leaves and are typically found in open situation. Both extremes are connected by intermediate forms, and, in some instances, the development from the normal verrucose form into the sorediate form can be observed on one and the same thallus.

Selected specimens examined: San José: Braulio Carillo National Park, former section Carillo, »Botella« trail, 10° 09' N, 83° 58' W, 750 m, primary lower montane rain forest, 91-3194 (LG), 91-3236 (hb. Lücking). Alajuela: Caño Negro National Wildlife Refuge, 10° 54' N, 84° 47' W, 50 m, forest margin, 92-3009 (B); *ibid.*, *Citrus*, *Mangifera*, *Eugenia* and *Pachira* trees at ranger station, 92-2932 (CR), 92-2942 (M), 92-2970 (hb. Lücking). Alberto Brenes Biological Reserve, 10° 13' N, 84° 36' W, 850-900 m, primary lower montane rain forest, 91-565 (M), 91-1472 (GZU), 91-1479 (CR), 91-1480 (STU), 91-1488 (hb. Lücking). Heredia: La Selva Protection Zone, 10° 26' N, 84° 03' W, 50-100 m, primary lowland rain forest on CES/LOC/CEN trails, 91-5149 (NY); *ibid.*, forest margin on SHO trail, 91-2504 (UPS), 91-2610 (hb. Lücking). Cartago: Alto La Gloria, Interamerican highway, 9° 48' N, 83° 57' W, 1700 m, gallery forest, 91-3598 (STU), 91-3622 (G). Centro Agronómico Tropical de Investigación y Enseñanza (C.A.T.I.E.), section Florencia, 9° 53' N, 83° 41' W, 700-750 m, secondary forest, 91-3673 (GZU, LG, STU). Puntarenas: Corcovado National Park, »Los Patos« to »Sirena« trail, 8° 31' N, 83° 34' W, 50-100 m, primary lowland rain forest, 92-3699 (VBI). El Ceibo, 8° 50' N, 82° 52' W, 1100 m, *Citrus* and *Mangifera* trees in village, 91-4048

(UPS). Limón: Barra del Colorado National Wildlife Refuge, 10° 46' N, 83° 36' W, sea level, primary lowland rain forest, 92-2406 (BM). Braulio Carillo National Park, section Quebrada Gonzales, »Botarrama« trail, 10° 12' N, 83° 55' W, 480 m, primary submontane rain forest, 91-1574 (hb. Kalb, hb. Lücking), 92-4156 (CBG, NY). Tortuguero National Park, 10° 32' N, 83° 30' W, sea level, primary lowland rain forest, 92-1845 (B, CR, M), 92-1846 (GZU, LG, UPS); *ibid.*, Cerro Tortuguero, 10° 35' N, 83° 31' W, 0-100 m, primary lowland rain forest, 92-2555 (UPS), 92-2627 (CR).

***Fellhanera subfuscatula* R. Lücking sp.n.**

Fellhanera fuscatula auct., non (Müll. Arg.) Vezda.

A *Fellhanera fuscatula* ascospores 5-septate differt.

Typus: PARAGUAY. Cordillera de Mbatobi, 1887, Balansa 4255 (G holotype).

Description: Differing from *Fellhanera fuscatula* sensu meo (see above; = *F. dominicana* sensu Santesson 1952) by the predominantly 5-septate ascospores. Thallus and apothecial morphology and anatomy, as well as pycnidia and conidia, similar to *F. fuscatula*.

Etymology: The name refers to its close relationship to *Fellhanera fuscatula*.

Notes: The new epithet for this well-known species is introduced since all the type material of *Fellhanera fuscatula* sensu Santesson (1952) and its synonyms proved to have 7-septate ascospores and hence are identical with the taxon known as *F. dominicana* sensu Santesson (see above). The question arises whether it was necessary to introduce a new name at all, since both taxa are only separated by their ascospore type, but that separation is supported by different distribution patterns: *F. fuscatula* sensu meo (7-septate) being most common in the Neotropics, and *F. subfuscatula* (5-septate) in tropical Africa. Further, the thallus in *F. fuscatula* sensu meo is more often smooth, and the apothecia are often provided with a thin margin, while *F. subfuscatula* usually has a finely farinose thallus, and the apothecial margin is more often reduced in mature apothecia.

The material from Paraguay has been se-

lected as type for *Fellhanera subfuscatula* since it is comparatively well developed and exhibits the typical characteristics, particularly the constantly 5-septate ascospores and the pycnidia with bacillar conidia (see below *F. fuscatula* for further discussion).

Selected specimens examined: COSTA RICA. San José: Las Quebradas, 9° 26' N, 83° 42' W, 900-1000 m, *Citrus* trees and coffee plantation, 92-4290, 92-4291 (hb. Lücking). Limón: Cahuita National Park, section Kelly Creek, 9° 44' N, 82° 50' W, sea level, coastal lowland rain forest, 91-2953 (hb. Lücking). Puntarenas: Corcovado National Park, »Sirena« to Rio Claro trail, 8° 28' N, 83° 35' W, 50-150 m, primary and secondary lowland rain forest, 92-3501 (hb. Lücking). Limón: Braulio Carrillo National Park, section Quebrada Gonzales, »Botarrama« trail, 10° 12' N, 83° 55' W, 480 m, forest margin, 91-308 (hb. Lücking).

**Fellhanera sublecanorina* (Nyl.) Vezda

Selected specimens examined: San José: Las Quebradas, 9° 26' N, 83° 42' W, 1000-1100 m, primary and secondary montane rain forest, 92-4337 (hb. Lücking, with *F. stanhopeae*), 92-4341 (NY), 92-4359 (CBG, G, STU, ULM). Cartago: Guayabo National Monument, 9° 59' N, 83° 43' W, 850-900 m, secondary forest, 92-1425 (UPS, hb. Kalb), 92-1615 (B, M), 92-1616 (GZU), 92-1617 (LG), 92-1800 (CR). Jicotea, 9° 49' N, 83° 32' W, 900 m, *Citrus* trees on finca, 91-1305 (hb. Lücking).

Fellhanera subternella (Nyl.) Vezda

Selected specimens examined: San José: Braulio Carrillo National Park, section La Hondura, 10° 02' N, 84° 00' W, 1500 m, primary montane rain forest and forest margin, 92-4765 (hb. Lücking), 92-4770 (M). Las Quebradas, 9° 26' N, 83° 42' W, 900-1000 m, *Citrus* trees and coffee plantation, 92-4297 (hb. Lücking). Cartago: Guayabo National Monument, 9° 59' N, 83° 43' W, 850-900 m, secondary forest, 92-1903 (hb. Lücking). Tapanti National Wildlife Refuge, »La Pava« trail, 9° 46' N, 83° 47' W, 1500-1700 m, primary montane to upper montane rain forest, 92-30 (hb. Lücking). Limón: Braulio Carrillo National Park, section Quebrada Gonzales, »Botarrama« trail, 10° 12' N, 83° 55' W, 480 m,

canopy layer, 91-1302 (hb. Lücking). Hitoy Cerere Biological Reserve, 9° 41' N, 83° 02' W, 100 m, *Citrus* and *Mangifera* trees at station, 91-1281 (hb. Lücking).

Fellhanera verrucifera R. Lücking sp.n. (Fig. 4E, 6F)

Thallus epiphyllus, tenuissimus, continuus, viride ad fusco-cinereus, verrucis numerosis pallide virido-cinereis et 0.02-0.03 mm diam. instructus. Apothecia 0.2-0.35 mm diam., rotundata, basi constricta; discus planus, cinereo-niger ad fuscus, albo-pruinosis ad nudus. Excipulum paraplectenchymaticum, incoloratum. Hypothecium fuscum; pars basalis apothecii aeruginosa. Hymenium incoloratum; epithecium indistinctum. Paraphyses leviter ramoso-connexae. Asci clavati, ad typum *Byssoloma* pertinentes. Ascospores 8-nae, 5(-7)-septatae, oblongo-fusiformes ad bacillares, 20-28 × 3.5-4 µm. Alga ad Chlorococceas pertinens.

Typus: COSTA RICA. Heredia: La Selva Protection Zone, 10° 26' N, 84° 03' W, 50-100 m, primary forest on CES/LOC/CEN trail, on leaves of a dicotyledon, II. 1992, leg. R. Lücking 92-60 (ULM holotype).

Description: Thallus epiphyllous, thin, continuous, up to 15 mm across, finely and densely verrucose, brownish to greenish grey, verrucae 0.02-0.03 mm diam., pale greenish to yellowish grey. Phycobiont a species of Chlorococceae, cells 5-8 µm diam.

Apothecia 0.2-0.35 mm diam. and 0.1-0.13 mm high, at first rounded, with a plane, greyish black to dark brown disc usually provided with a very thin, yellowish white pruina (rarely naked), and with a distinct, slightly prominent, pale grey to chamois-coloured margin, later with a plane to convex, dark brown to chocolate brown, thinly pruinose or naked disc, and with the margin disappearing. Exciple distinctly paraplectenchymaticous, colourless, cells 3-5 µm diam. Hypothecium rather dark brown, 20-25 µm high; central apothecial base aeruginous. Hymenium up to 50 µm high, colourless. Epithecium indistinct. Paraphyses 0.07 µm thick, slightly branched and anastomosing. Asci clavate, 35-45 × 8-13 µm, of the *Byssoloma* type. Ascospores 8 per ascus, 5(-7)-septate, oblong-fusiform to almost bacillar,

colourless, $20-28 \times 3.5-4 \mu\text{m}$.

Pycnidia not seen.

Etymology: The specific epithet refers to the verrucose thallus.

Notes: This new species is immediately recognized by its thinly verrucose thallus. Among *Fellhanera*, verrucose thalli are only found in *F. stanhopeae*, *F. lambinonii*, and *F. badimoides*, but here the verrucae are much larger (c. $0.07-0.15 \text{ mm diam.}$). A thallus structure similar to *F. verrucifera* is found in *Bacidia brasiliensis* (Müll. Arg.) Zahlbr. (Santesson 1952), and these species might be confused externally. However, *B. brasiliensis* has much larger apothecia, and the apothecial anatomy (paraphyses, ascus type, ascospores) is completely different.

F. verrucifera is perhaps closely related to *F. fuscata*, which has similar ascospores and apothecia, but lacks a pruina and thallus verrucae. On the other hand, the often pruinose apothecia and the characteristic colour change between young and mature apothecia (greyish black and with distinct margin vs. dark brown and without margin) refer this species to a group formed by *F. santessonii*, *F. winkleriana* and *F. muhlei*. All these species have very similar apothecia, but differ in their thallus structure (smooth, verrucose, or sorediate) and their ascospores (3-septate or 5-7-septate).

Additional specimens examined: Alajuela: Caño Negro National Wildlife Refuge, $10^{\circ} 54' \text{N}$, $84^{\circ} 47' \text{W}$, 50 m, isolated primary lowland rain forest, 92-2749 (LG). Heredia: La Selva Protection Zone, $10^{\circ} 26' \text{N}$, $84^{\circ} 03' \text{W}$, 50-100 m, primary lowland rain forest on CES/LOC/ CEN trails, 91-5164 (hb. Lücking). Puntarenas: Corcovado National Park, »Los Patos«, $8^{\circ} 34' \text{N}$, $83^{\circ} 31' \text{W}$, 50-150 m, primary lowland rain forest, 92-3117 (GZU). Limon: Braulio Carillo National Park, section Quebrada Gonzales, »Botarrama« trail, $10^{\circ} 12' \text{N}$, $83^{\circ} 55' \text{W}$, 480 m, primary submontane rain forest, 91-1304, 92-4996 (both hb. Lücking).

Fellhanera viridis R. Lücking sp.n. (fig. 50c in Lücking 1992a)

Fellhanera viridis nom. nud. in Lücking, R., *Beih. Nova Hedwigia* 104: 136 (1992).

Thallus epiphyllus, tenuissimus, continuus, laevigatus vel farinoso-granulosus, viridis, sorediis pallide viridibus instructus. Apothecia $0.2-0.25 \text{ mm diam.}$, rotundata, basi constricta; discus planus, fuscus ad rubro-fuscus; margo distinctus, pallidior. Excipulum paraplectenchymaticum, incoloratum. Hypothecium incoloratum ad pallide flavescens. Hymenium incoloratum. Paraphyses ramoso-connexae; asci clavati, ad typum *Byssoloma* pertinentes. Ascospores 2-4(-8)-nae, 3-septatae, oblongo-ellipsoideae, $15-20 \times 4-5 \mu\text{m}$. Alga ad Chlorococcaceas pertinens.

Typus: COSTA RICA. Limon: Cahuita National Park, section Puerto Vargas, $9^{\circ} 44' \text{N}$, $82^{\circ} 49' \text{W}$, sea level, coastal forest, on leaves of Zingiberaceae, XI. 1987, leg. R. Lücking 87-272 (ULM holotype).

Description: Thallus epiphyllous, thin, continuous, up to 10 mm diam., smooth to farinose or granulose, green, provided with pale green soralia. Soralia at first circular and up to 0.3 mm in diam., later irregular and confluent. Soredia when young $10-15 \mu\text{m diam.}$, with one rather large algal cell ($5-7 \mu\text{m}$), later up to $20 \mu\text{m diam.}$ and with several smaller ($3-5 \mu\text{m}$) algal cells, wrapped up with rather thin, colourless hyphae. Phycobiont a species of Chlorococcaceae, cells $5-8 \mu\text{m diam.}$

Apothecia very rare, $0.2-0.25 \text{ mm diam.}$ and 0.1 mm high , rounded, with a plane, light brown to brown or reddish brown disc and distinct, chamois-coloured margin. Exciple distinctly paraplectenchymatous, colourless, cells $3-7 \mu\text{m diam.}$ Hypothecium colourless to pale yellowish, hardly delimited from the basal exciple, $15-30 \mu\text{m high}$. Hymenium $35-40 \mu\text{m high}$, colourless. Paraphyses $0.07-1 \mu\text{m thick}$, branched and anastomosing. Asci clavate, $35-40 \times 8-11 \mu\text{m}$, of the *Byssoloma* type. Ascospores 2-4(-8) per ascus, often depauperate, 3-septate, oblong-ellipsoid, colourless, $15-20 \times 4-5 \mu\text{m}$.

Pycnidia not seen.

Etymology: The specific epithet refers to the vivid, green colour of the thallus.

Notes: *Fellhanera viridis* is formally described here with some hesitation. The material is scanty, with only a few apothecia present. The sorediate

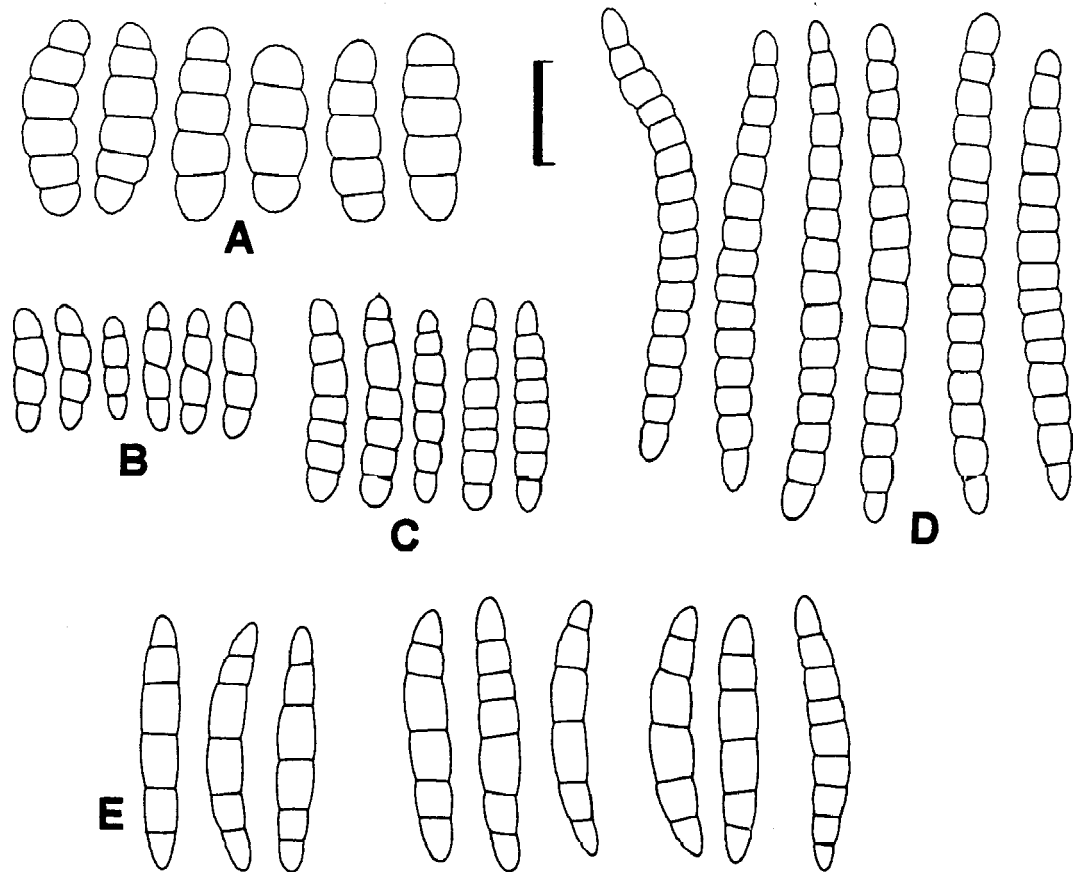


Figure 4. (A) *Fellhanera* sp. A [92-2720]. (B) *Fellhanera* sp. B [92-449]. (C) *Fellhanera* sp. C [92-447]. (D) *Fellhanera* sp. D [92-403]. (E) *F. verrucifera* [holotype]. Ascospores. Scale = 10 μ m.

thallus is similar to that of *F. muhleii*, its green colour alone being no distinctive feature which would justify a separation from the latter. Its apothecia are, however, different in having a non-pruinose, light brown disc and an almost colourless hypothecium. Whereas *F. muhleii* has its non-sorediate counterpart in *F. santessonii*, that of *F. viridis* is to be found in the *F. rhapsidophylli* aggregate. I am convinced that *F. viridis* represents a good taxon, but further collections are necessary to establish its full range of variation, especially regarding apothecium and ascospore

sizes, and the instable number of ascospores per ascus.

Fellhanera viridis is also reminiscent of the recently described *F. seroexpectata* Sérus. (Sérusiaux 1996), differing in the greenish instead of yellowish soralia and the light brown apothecia. A remarkable feature of both species, also found in *F. muhleii*, is the irregular number of ascospores per ascus, and the occurrence of depauperate ascospores. This might be explained by predominantly vegetative dispersal via soredia, which decreases the selective pressure on sexual reproduction, allowing detrimental genetical

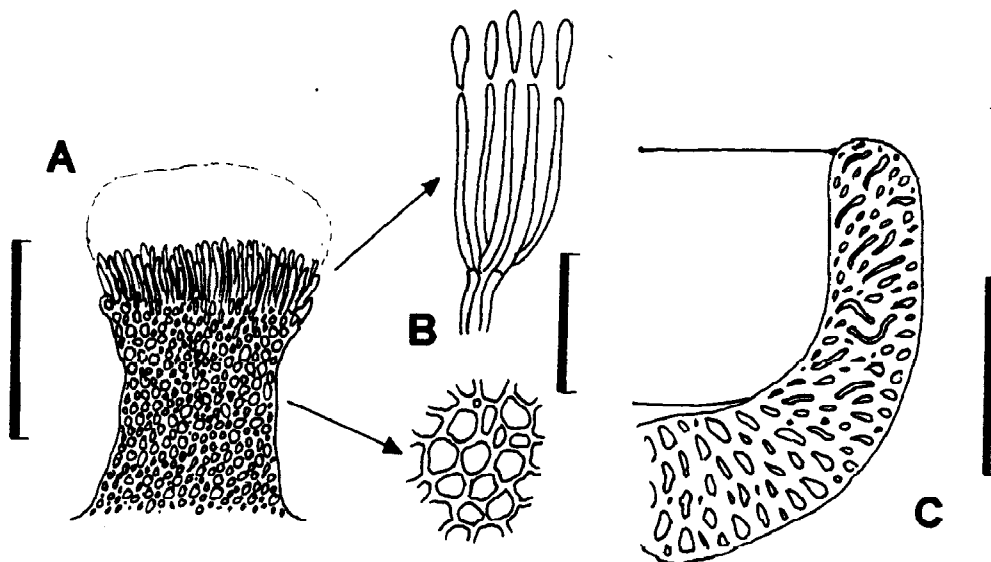


Figure 5. (A-B) *Fellhanera pilomarginata* [an isotype], in (A) section through pycnidium, in (B) sockle and conidiogenous layer enlarged. (C) *F. montana*, section through lateral exciple. Scale in (A) = 50 μm , in (B) = 10 μm , in (C) = 100 μm .

modifications on the development and number of ascospores to persist. This might finally lead to the complete suppression of sexual reproduction and the formation of apomictic strains.

Fellhanera sp. A

Notes: This and the following three species belong to a group characterized by their dark greyish black to pure black apothecia, their aeruginous colour in parts of the hypothecium and exciple, and their richly branched and anastomosing paraphyses. In certain respects they resemble the genus *Tapellaria*, but differ clearly by their continuous, farinose to granulose thalli. They may represent well separated, autonomous species, but the scanty material does not allow formal descriptions. The species are discussed in detail here in order to alert potential collectors and taxonomists working with the group. All taxa where found at higher elevations, which are obviously undercollected and hide a rich foliicolous lichen flora still to be discovered.

Fellhanera sp. A is characterized by its farinose to granulose, pale yellowish grey thallus and its blackish grey apothecia with a paler grey

margin. The exciple is colourless or slightly aeruginous laterally, the hypothecium blackish brown, with an aeruginous tinge, and the epithecium colourless to slightly aeruginous. The ascospores are irregularly 3-5-septate, 15-20 \times 4-6 μm large, and slightly constricted at the septa. The only known species of *Fellhanera* which comes close in appearance is *F. christiansenii* Sérus. & Vezda, which differs mainly in its dark reddish brown hypothecium and its distinctly brown exciple.

Specimens examined: COSTA RICA. San José: Chirripó National Park, 9° 28' N, 83° 33' W, 3000-3200 m, primary cloud forest below »Hopeless Mountain«, 92-547 (hb. Lücking). Cartago: Tapanti National Wildlife Refuge, 9° 44' N, 83° 47' W, 2200 m, forest margin at embankment of the Rio Macho, 92-2720 (hb. Lücking).

Fellhanera sp. B

Notes: This taxon is in several respects (exciple, hypothecium, epithecium) similar to *Fellhanera* sp. A, but differs in its pure black apothecia (including their margin) and its regularly 3-septate, smaller ascospores, being 12-15 \times 3-3.5 μm in size.

Specimens examined: COSTA RICA. San José: Chirripó National Park, 9° 28' N, 83° 34' W, 1800-2200 m, primary upper montane rain forest, 92-321 (hb. Lücking); *ibid.*, 9° 28' N, 83° 32' W, 2550-2800 m, primary cloud forest, 92-449 (hb. Lücking).

Fellhanera sp. C

Notes: *Fellhanera* sp. C is also similar to *Fellhanera* sp. A, but differs in its smooth to minutely farinose thallus and its regularly 7-septate ascospores measuring c. $20 \times 3.5 \mu\text{m}$. The ascospores are identical with those of *F. fuscata*, which may be the closest ally of the present taxon but differs by the light to dark brown apothecia.

Specimen examined: COSTA RICA. San José: Chirripó National Park, 9° 28' N, 83° 32' W, 2550-2800 m, primary cloud forest, 92-447 (hb. Lücking).

Fellhanera sp. D

Notes: This taxon is characterized by its yellowish grey, farinose to granulose thallus and its black apothecia with a colourless exciple, a purplish black hypothecium, and a blackish brown epithecium. The hymenium is partly aeruginous. The most distinctive feature is its ascospores, which are vermiform, 15-septate and $40\text{-}50 \times 4\text{-}4.5 \mu\text{m}$ large. The apothecial anatomy is very similar to that of *Tapellaria molleri* (Henriques) R. Sant., but the thallus structure and other features refer to *Fellhanera*, where the species finds a counterpart in *F. longispora*.

Specimen examined: COSTA RICA. San José: Chirripó National Park, 9° 28' N, 83° 33' W, 2200-2550 m, primary upper montane rain forest, 92-403 (hb. Lücking).

ECOLOGICAL OBSERVATIONS

The species of *Fellhanera* show two remarkable ecological tendencies, as obvious from the collection data presented in this paper: (1) Many species extend into, or prefer, montane regions, and (2) almost all species are restricted to primary forest (see Lücking 1992b, c). Typical representatives of, and confined to, the lowland primary forest in

Costa Rica are *F. angustispora*, *F. badimoides*, *F. lisowskii*, *F. muhleii*, *F. rhapsidophylli*, and *F. verrucifera*. Another seven species also occur in the lowland primary forest, but extend into the submontane (*F. dictyospora*, *F. subfuscata*, *F. pilomarginata*, *F. longispora*) or montane forest belt (*F. fuscata*, *F. emarginata*, *F. santessonii*). The three closely related species, *F. rhapsidophylli*, *F. subfuscata*, and *F. fuscata*, show slightly different altitudinal preferences, which seem to correlate with ascospore septation: the higher the number of ascospore septa, the higher the altitudinal range of the species. Confined to the submontane or montane forest belt are *F. dispersa*, *F. elliotii*, *F. misionensis*, *F. paradoxa*, *F. montana*, and the four undescribed species with blackish apothecia, *Fellhanera* sp. A-D. Thallus morphology seems to correlate with altitudinal preferences as well: lowland species or individuals of species with wide altitudinal range more often have smooth thalli, while those representatives of montane habitats exhibit farinose to granulose thalli. The latter might be an adaptation to water uptake by fog.

A few species occur principally in primary forest but may also be found in semi-open secondary vegetation, viz. *F. rubida*, *F. semecarpi*, *F. stanhopeae*, and *F. sublecanorina*. Two further species, *F. bouteillei* and *F. subternella*, are mainly found in semi-open to open secondary vegetation, or in the canopy of primary forests. All have a rather broad altitudinal range, with *F. bouteillei* occurring up to the forest limit (3000-3500 m alt.). Concentrated among these taxa are those with bluish, farinose to granulose thalli, supposedly containing secondary compounds (Lücking et al. 1994).

The preference of *Fellhanera* species for primary forest, together with the rarity of several taxa, indicates this genus as particularly threatened by the destruction of natural forests in the tropics. On the other hand, high specific diversity of *Fellhanera* at a particular site is a good indicator of a low level of disturbance.

NOTES ON INFRAGENERIC RELATIONSHIPS WITHIN *FELLHANERA*

As stated in the Introduction, the present number

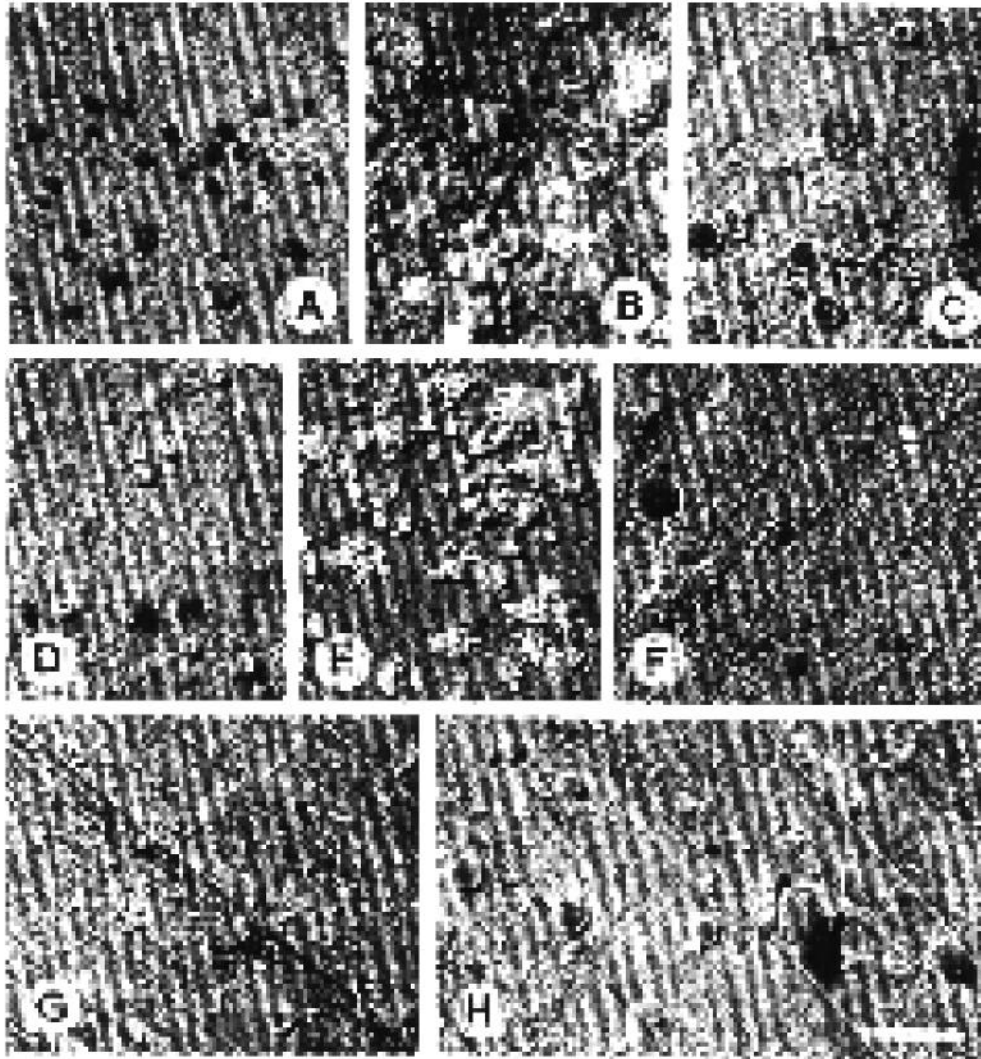


Figure 6. (A) *Fellhanera emarginata* [91-1285]. (B) *F. dispersa* [an isotype]. (C) *F. longispora* [92-2014]. (D-E) *F. muhleii* [92-2754], in E showing soralia. (F) *F. verrucifera* [holotype]. (G-H) *F. pilomarginata* [an isotype], in G showing pycnidia. General habit. Scale = 1 mm.

of accepted species in *Fellhanera* may still not reflect its actual diversity. In addition, the generic delimitation within the Pilocarpaceae and the number of genera to be accepted in that family are not yet settled. Therefore, the statements on infrageneric relationships within *Fellhanera* can only be regarded as provisional, particularly as the concentrate on the foliicolous taxa. The reason why they are given here are (1) to provide a survey over the diversity of characters and their distribution patterns, in order to facilitate taxonomic access to the genus, and (2) to identify core groups, in order to create a base for further systematic studies in the genus and to facilitate selection of taxa to be used in molecular and cladistic approaches.

Before going into details, it should be stressed that a number of species presently placed in *Fellhanera* do not share all characters typical of that genus. This accounts in particular for three species described in the present paper, viz. *Fellhanera angustispora*, *F. emarginata*, and *F. pilomarginata*. The reasons why, for the time being, they have been placed in *Fellhanera*, are discussed above. Other species, such as *F. stanhopeae* or *F. vandenberghenii*, deviate in their excipular structure or their pycnidia but are closely related to typical representatives of the genus (Lücking et al. 1994). Besides the excipular structure, the variation in the structure of pycnidia and types of conidia certainly deserves attention in further generic or subgeneric divisions, as already exemplified by the erection of the genus *Fellhaneropsis* (Sérusiaux 1996).

Most of the currently known 44 foliicolous species of *Fellhanera* can be assigned to two major groups and several aggregates (Table 1): the ***F. fuscata* group**, with the *F. fuscata*, the *F. christiansenii*, the *F. santessonii*, and the *F. endopurpurea* aggregate, and the ***F. subternella* group**, with the *F. subternella* and the *F. stanhopeae* aggregate. The ***F. fuscata* aggregate** is considered here as the centre of the genus, not only because it includes the generic type, but also because it consists of a large number of closely related species which share features frequently found in *Fellhanera*, viz. *F. encephalarti* (Vezda), *F. misionensis*, *F. rhapsidophylli*, *F. subfuscata*, *F. fuscata*, *F. longispora*, *F. paradoxa*, *F. elliottii*, and *F. dictyospora*. All are characterized by greenish grey thalli and brow-

nish apothecia with a well developed paraplectenchymatous exciple and a blackish-aeruginous apothecial base, as well as fusiform to bacillar conidia (as far as known at present). As in the genus *Tapellaria* (Santesson 1952), this group includes a complete series of ascospore types, from 1-septate (*F. misionensis*) via multiseptate (e.g. *F. fuscata*) and submuriform (*F. elliottii*) towards muriform (*F. dictyospora*). The genetic potential for the evolution of different ascospore types is exemplified by *F. paradoxa*, where ascospores of very different size and septation can be found within the same hymenium or ascus. The most frequent species of this group have a pantropical distribution, although with emphasis on different tropical regions: *F. rhapsidophylli* is most common in tropical Asia, *F. subfuscata* mainly restricted to tropical Africa, and *F. fuscata* most abundant in the Neotropics.

Several species are close to this aggregate but are characterized by particular features. These are *Fellhanera seroexpectata* Sérus. and *F. viridis*, both with sorediate thalli, and *F. vandenberghenii* (Sérus.) Vezda, which differs from *F. misionensis* mainly by its flask-shaped pycnidia. All seem to have rather restricted distributions in Central America, Europe, and Africa, respectively.

The species of the ***Fellhanera christiansenii* aggregate**, i.e. *F. christiansenii* Sérus. & Vezda, and four undescribed taxa mentioned in the present paper, differ from the *F. fuscata* aggregate by their blackish apothecia. This group needs further study, since its diversity is hardly known at present. It is not necessarily a natural group, since species with blackish apothecia may have evolved independently. Indeed, every of the taxa included here finds an ascospore counterpart in the *F. fuscata* aggregate.

The ***Fellhanera santessonii* aggregate** is formed by *F. santessonii*, *F. muhleii*, *F. winkleriana*, *F. ekmanii* (Vezda) R. Lücking, and *F. verrucifera*. These species usually have a smooth thallus and apothecia with a particular colour and development. The young apothecia are usually greyish black, with a whitish pruina and a rather distinct, prominent, whitish margin. The mature apothecia are more brownish, the pruina becomes yellowish white and often disappears, and the margin is reduced. *F. muhleii* differs from *F. santessonii* by its well developed thallus

and the formation of soralia, and *F. winkleriana* by its larger, 5-septate ascospores. *F. ekmanii* is characterized by crystals which are externally deposited on the otherwise paraplectenchymatous exciple, and by its mainly hypophyllous apothecia. Whereas *F. santessonii*, *F. muhleii*, *F. winkleriana*, and *F. verrucifera*, seem to represent a close, natural entity, *F. ekmanii* shows affinities towards the *F. stanhopeae* group, particularly *F. avilezii*. All species are only known from the Neotropics.

The *Fellhanera endopurpurea* aggregate comprises four species with basically smooth thalli and apothecia with a distinct reddish tinge, the hypothecium usually reacting K+ purplish red. It includes *F. congesta* (Vezda) Vezda (ascospores 1-septate), *F. endopurpurea* Hafellner & Vezda and *F. wirthii* (Vezda) Vezda (ascospores 3-septate), and *F. microdiscus* (Vain.) Vezda (ascospores 5-septate). All are known from the Paleotropics.

A very characteristic and probably natural group with a high morphological diversification is the *Fellhanera subternella* group, with most species sharing pyriform conidia and the presence of secondary substances, such as usnic acid, isousnic acid, and zeorine (Tønberg 1992; Lücking et al. 1994). The species of the *F. subternella* aggregate are characterized by their mainly bluish thalli and their pale yellowish to vividly orange-yellow apothecia. Typical representatives are *F. bouteillei* (ascospores 1-septate), *F. subternella*, *F. aurantiaca* (Vezda) Vezda and *F. carnea* (Vezda) Vezda (ascospores 3-septate), and *F. solediantha* (Vezda) Vezda (thallus solediate). *F. parvula* (Vezda) Vezda and *F. subtilis* (Vezda) Diederich & Sérus. may also belong here, but this remains to be tested. Two further species, viz. *F. lisowskii* and *F. badimioides*, with smooth to verrucose thalli, provide a transition towards the supposedly related genus *Badimia* (Lücking et al. 1994).

The related *Fellhanera stanhopeae* aggregate includes *F. stanhopeae*, *F. lambinonii*, *F. sublecanorina*, *F. avilezii*, and some further, still undescribed taxa. Apart from their thallus chemistry, the species are basically characterized by their dark apothecia with a usually well developed pale margin, and the tendency to deposit crystals in the exciple, making its structure hard to distinguish (Lücking et al. 1994). *F. stanhopeae*

has a distinctly green thallus with large crystalline verrucae which may break up into soralia, and a crystalline exciple. The closely related *F. lambinonii* is externally very similar, but differs in the absence of crystals in the exciple and the more elaborated soralia. A similar variation is found in the couple *F. sublecanorina*, with paraplectenchymatous exciple, and a still undescribed, externally identical species with crystalline exciple found in collections from Guyana (H. Sipman, pers. comm. 1995).

Finally, there are two heterogeneous entities whose affinity is difficult to establish. The *Fellhanera dispersa* group comprises four species with a smooth thallus composed of dispersed, rounded patches, a rare feature within the genus. The closely related *F. semecarpi* and *F. pauciseptata*, with ochraceous to reddish brown apothecia, are certainly allied to species of the *F. fuscicula* or *F. endopurpurea* aggregate. The other two species, *F. dispersa* and *F. bullata* Kalb & Vezda, stand a bit more isolated, though their affinity to *Fellhanera* is perfectly clear.

The *Fellhanera emarginata* group comprises *F. emarginata* and *F. angustispora*. Both are characterized by the completely reduced exciple. Although showing distinct affinities towards the *F. fuscicula* group, these species are also akin to the genus *Byssoloma*, particularly *B. minutissimum* Kalb & Vezda and its relatives. This is also true of *F. pilomarginata*, a species with an excipular type intermediate between *Fellhanera* and *Byssoloma*, and with a particular anamorph not found in other species of *Fellhanera*.

Three characters which deserve attention are the soledia, the pycnidia, and the secondary chemistry. Soledia are rare among foliicolous lichens but relatively common in the genus *Fellhanera*. Their formation is not restricted to a particular group but found in species of different affinities, e.g. *F. seroexpectata* and *F. viridis* in the *F. fuscicula* aggregate, *F. muhleii* in the *F. santessonii* aggregate, *F. lambinonii* in the *F. stanhopeae* aggregate, and *F. solediantha* in the *F. subternella* aggregate, indicating that their evolution is likely to occur independently. A feature of much higher taxonomic value are the pycnidia and conidia. The pyriform conidia typical of the Pilocarpaceae (Vezda 1986) are principally found in *Byssoloma* and the *Fellhanera*

Table 1. Proposal for subgeneric division of the genus *Fellhanera*, based on the presently accepted 44 foliicolous species (Lücking 1991, 1992a; Lücking et al. 1994; Lücking & Lücking 1995; Sérusiaux 1996; and the present paper). The principal characteristics are indicated to facilitate rapid distinction between taxa on the same level. If not otherwise stated, the thallus of a given species is smooth to farinose and lacks distinctive features such as soralia or verrucae. Formal subgeneric ranks are not introduced since the genus needs further study, but in such a treatment, the groups indicated here might appropriately receive sectional status, while the aggregates would refer to series.

Fellhanera s.l. (exclave modified or reduced but not of the *Byssoloma* type)

***Fellhanera angustispora* R. Lücking**

(ascospores 3-septate, narrow)

***Fellhanera emarginata* R. Lücking**

(ascospores 3-septate, broad)

***Fellhanera pilomarginata* R. Lücking**

Fellhanera s.str. (exclave paraplectenchymatous)

Fellhanera fuscata group (conidia fusiform or bacillar, secondary substances usually absent)

Fellhanera fuscata aggregate (apothecia brownish)

***Fellhanera encephalarti* (Vezda) Vezda**

(ascospores 1-septate, small)

***Fellhanera misionensis* Ferraro & R. Lücking ined.**

(ascospores 1-septate, medium-sized)

***Fellhanera vandenberghenii* (Sérus.) Vezda**

(ascospores 1-septate, pycnidia beaked)

***Fellhanera rhapsidophylli* (Rehm) Vezda**

(ascospores 3-septate)

***Fellhanera seroexpectata* Sérus.**

(ascospores 3-septate, thallus sorediate, apothecia dark brown)

***Fellhanera viridis* R. Lücking**

(ascospores 3-septate, thallus sorediate, apothecia light brown)

***Fellhanera subfuscata* R. Lücking**

(ascospores 5-septate)

***Fellhanera fuscata* (Müll. Arg.) Vezda**

(ascospores 7-septate)

***Fellhanera longispora* R. Lücking**

(ascospores 9-11-septate)

***Fellhanera paradoxa* (Vezda) Vezda**

(ascospores irregularly septate, broad)

***Fellhanera elliotii* (Vain.) Vezda**

(ascospores submuriform)

***Fellhanera montana* R. Lücking**

(ascospores muriform, small, eight per ascus)

***Fellhanera dictyospora* R. Lücking**

(ascospores muriform, large, single)

Fellhanera endopurpurea aggregate (apothecia reddish brown, hypothecium K+ purplish)

***Fellhanera congesta* (Vezda) Vezda**

(ascospores 1-septate)

***Fellhanera endopurpurea* Hafellner & Vezda**

(ascospores 3-septate)

- Fellhanera wirthii* (Vezda) Vezda**
(ascospores 3-septate)
- Fellhanera microdiscus* (Vain.) Vezda**
(ascospores 5-septate)
- Fellhanera christiansenii* aggregate (apothecia greyish black)
- Fellhanera christiansenii* Sérus. & Vezda**
(ascospores 3-septate, thallus soresiate)
- Fellhanera* sp. A** (ascospores 3-5-septate)
- Fellhanera* sp. B** (ascospores 3-septate)
- Fellhanera* sp. C** (ascospores 7-septate)
- Fellhanera* sp. D** (ascospores 15-septate)
- Fellhanera santessonii* aggregate (apothecia brownish black, pruinose)
- Fellhanera santessonii* Barillas & R. Lücking**
(ascospores 3-septate)
- Fellhanera muhleii* R. Lücking**
(ascospores 3-septate, thallus soresiate)
- Fellhanera winkleriana* R. Lücking**
(ascospores 5-septate)
- Fellhanera ekmanii* (Vezda) R. Lücking**
(ascospores 5-septate, exciple with crystals)
- Fellhanera verrucifera* R. Lücking**
(ascospores 5-7-septate, thallus verrucose)
- Fellhanera subternella* group (conidia pyriform, secondary substances usually present)
- Fellhanera subternella* aggregate (apothecia pale yellowish to orange-brown)
- Fellhanera bouteillei* (Desm.) Vezda**
(ascospores 1-septate, apothecia large)
- Fellhanera parvula* (Vezda) Vezda**
(ascospores 1-septate, apothecia small)
- Fellhanera rubida* (Müll. Arg.) R. Lücking**
(ascospores 3-septate, apothecia brownish, thallus greenish)
- Fellhanera subternella* (Nyl.) Vezda**
(ascospores 3-septate)
- Fellhanera carnea* (Vezda) Vezda**
(ascospores 3-septate)
- Fellhanera subtilis* (Vezda) Diederich & Sérus.**
(ascospores 3-septate)
- Fellhanera aurantiaca* (Vezda) Vezda**
(ascospores 3-septate, exciple K+ orange red)
- Fellhanera soresdiantha* (Vezda) Vezda**
(ascospores 3-septate, thallus soresiate)
- Fellhanera lisowskii* (Vezda) Vezda**
(ascospores 3-septate, thallus smooth)
- Fellhanera badimoides* R. Lücking, Lumbsch & Elix**
(ascospores 3-septate, thallus verrucose)
- Fellhanera stanhopeae* aggregate (apothecia brownish black)
- Fellhanera lambinonii* (Sérus.) R. Lücking & Sérus.**
(ascospores 3-septate, thallus verrucose-soresiate)
- Fellhanera stanhopeae* (Müll. Arg.) R. Lücking, Lumbsch & Elix**
(ascospores 3-septate, thallus verrucose-soresiate, exciple with crystals)

***Fellhanera sublecanorina* (Nyl.) Vezda**

(ascospores 3-septate, thallus smooth)

***Fellhanera avilezii* R. Lücking**

(ascospores 3-septate, apothecia pruinose, hypophyllous)

Fellhanera dispersa group (thallus dispersed)***Fellhanera semecarpi* (Vain.) Vezda**

(ascospores 1-septate, apothecia ochraceous)

***Fellhanera pauciseptata* (R. Sant.) R. Lücking**

(ascospores 1-3-septate, apothecia ochraceous)

***Fellhanera dispersa* R. Lücking**

(ascospores 3-septate, apothecia reddish brown)

***Fellhanera bullata* Kalb & Vezda**

(ascospores 3-septate, apothecia dark brown, thallus bullate)

subternella group, whereas in the *F. fuscata* group, as well as in the genus *Byssolecania*, the conidia are narrowly fusiform or oblong to bacillar. The secondary chemistry seems to correlate with the conidial type, and both characters might provide a base for subgeneric division of *Fellhanera* (see Table 1), while generic division on account of these characters, as recent trends suggest, would certainly be inappropriate.

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