

Ascospore diversity of bryophilous Hypocreales and two new hepaticolous Nectria species

Peter Döbbeler

To cite this article: Peter Döbbeler (2005) Ascospore diversity of bryophilous Hypocreales and two new hepaticolous Nectria species, *Mycologia*, 97:4, 924-934

To link to this article: <http://dx.doi.org/10.1080/15572536.2006.11832784>



Published online: 27 Jan 2017.



Submit your article to this journal [↗](#)



View related articles [↗](#)

Ascospore diversity of bryophilous Hypocreales and two new hepaticolous *Nectria* species

Peter Döbbeler¹

Ludwig-Maximilians-Universität München, Fakultät für Biologie, Systematische Botanik und Mykologie, Menzinger Straße 67, D-80638 München, Germany

Abstract: Hypocreales represents one of the most successful orders of ascomycetes on mosses and hepatics, and more than 30 obligately bryophilous species belonging to seven genera of Bionectriaceae and Nectriaceae are known. These fungi have a remarkably wide range of ascospore types that differ in form, size and septation. Especially heterogeneous are the ascospores of the six hypocrealean parasites recorded on European populations of *Frullania dilatata*. Patterns of distribution of bryophilous Hypocreales on this host appear to follow the principles of island biogeography. Two new leaf-perforating species of *Nectria* with unusual ascospores are described. *Nectria foertheri* Döbbeler sp. nov. grows biotrophically on *Porella* sp. in Guatemala, and *N. lagodes* Döbbeler sp. nov. is a necrotroph on *Frullania dilatata* in Italy and Greece.

Key words: ascospore morphology, bryophilous ascomycetes, *Frullania dilatata*, *Nectria foertheri*, *Nectria lagodes*

INTRODUCTION

More than 30 species in seven genera of Bionectriaceae and Nectriaceae (Hypocreales, Ascomycetes) are recorded on mosses and hepatics and nearly all are obligate parasites unknown from other substrates. Hypocrealean fungi comprise the most successful *fungi bryophili* with regard to species number, host range and geographic distribution. Although most are poorly known from herbarium material and only single or very few collections exist, substantial information on the teleomorphic stages is available (e.g. von Höhnelt 1919, Corner 1935, Hawksworth 1973, Racovitza 1959, Döbbeler 1978, 1998, 1999, 2004, Döbbeler and Carranza 1993, Rossman et al 1999). The bryophilous Hypocreales display a remarkably variable set of morphological, anatomical and ecological features indicating the group is taxonomically diverse. The tiny ascomata usually are restricted to dis-

tinct microniches on their hosts, such as ventral leaf borders or perianths in Jungermanniales or adaxial surfaces of leaves in Polytrichales. Several species regularly develop ascomata on the ventral side of foliose hepatics and perforate host leaves. Ascomata are globose or pyriform, setose or nonsetose, nonstromatic perithecia of varying size, and color varies from orange-red to hyaline. Excipulum structures represent a variety of tissue types. Hyphae offer additional important diagnostic features. They grow superficially over host cells, or between or within them, sometimes forming appresoria, haustoria or conidiogenous cells. The ecological relationships among fungal species and hosts range from biotrophic (with supra- or intercellular mycelium) to necrotrophic parasitism (with intracellular mycelium). At least one species causes malformations of infected host organs. Specificity to certain host species, genera or groups of host genera is pronounced in most species. Their diversity is highlighted by an array of ascospore features representing many types that occur within bryophilous ascomycetes in general (Döbbeler 1997, FIG. 1) and within the numerous nonbryophilous Hypocreales. In other cases the bryophilous Hypocreales have unique ascospores not recorded elsewhere within nectrioid fungi.

In this paper ascospore types of bryophilous species of *Nectria* and related genera are described and illustrated and an attempt is made to explain patterns in ascospore diversity by drawing correlations between ascospore types and ecological aspects. In addition two new hepaticolous species of *Nectria* with unusual ascospores are proposed.

MATERIAL AND METHODS

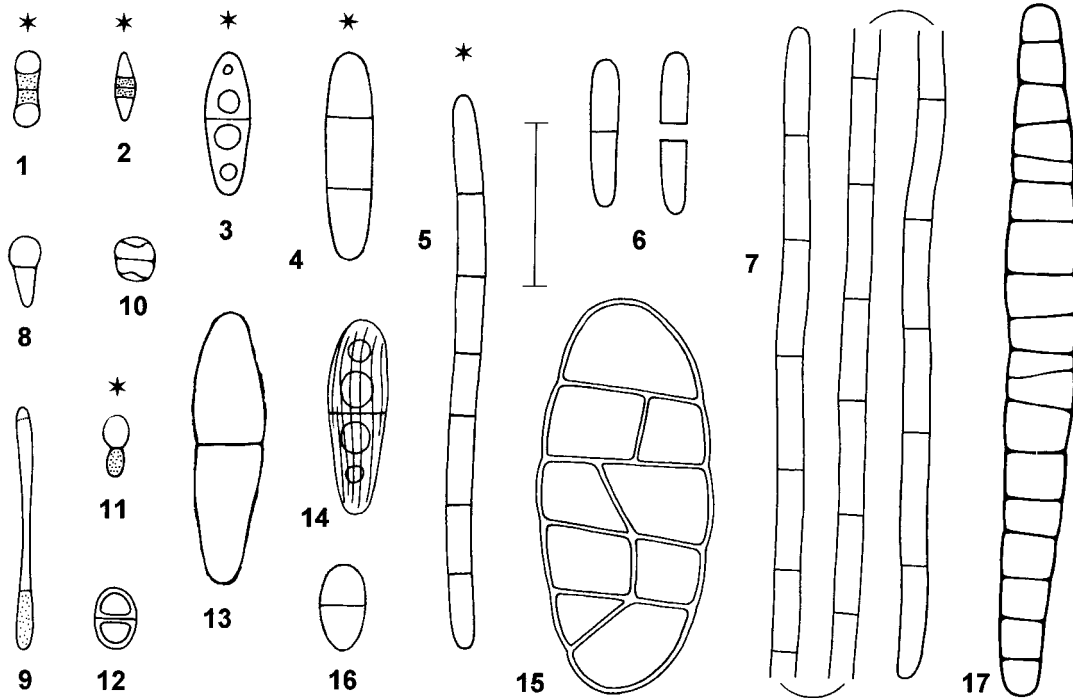
Measurements and illustrations of microscopic details were done in lactophenol-cotton blue (Merck 13741). Blue reactions of hyphae or spores in lactophenol-cotton blue are called cyanophilic or cyanophilous (Kotlaba and Pouzar 1964, Rambold 1995, Kirk et al 2001). Delicate structures such as apical paraphyses and ascospores of some species were analyzed with tap water and lactophenol-cotton blue as mounting media and different optical equipments (phase-contrast optics and differential interference contrast [DIC]).

DESCRIPTIONS OF ASCOSPORE TYPES

Unless otherwise stated the following species are known only from bryophytes. Ascospores are color-

Accepted for publication 29 June 2005.

¹ E-mail: doebbel@lrz.uni-muenchen.de



FIGS. 1–17. Ascospore diversity of bryophilous Hypocreales. 1. *Bryocentria brongniartii* (cyanophilic part stippled). 2. *Bryocentria metzgeriae* (cyanophilic part stippled). 3. *Bryonectria callicarpa*. 4. *Bryonectria* sp. 5. *Calonectria frullaniae*. 6. *Nectria brenesii* (disarticulating at the septum). 7. *Nectria byssophila*. 8. *Nectria contraria*. 9. *Nectria foertheri* (cell rich in plasmatic content stippled). 10. *Nectria gynophila*. 11. *Nectria lagodes* (cell with plasmatic content stippled). 12. *Nectria lankesteri*. 13. *Nectria muscivora* (epispor with cyanophilic warts). 14. *Nectria sanramonensis* (epispor with cyanophilic striations). 15. *Thyronectria hyperantarctica*. 16. *Ticonectria perianthii*. 17. *Trichonectria hirta*. All ascospores are drawn at the same magnification. An asterisk indicates ascospores of species growing on *Frullania dilatata*. Bar = 15 μm .

less and formed eight per ascus. Specimens examined and their herbarium location is given in parentheses.

Bryocentria brongniartii (P. Crouan et H. Crouan)

Döbbeler, Mycol Progr 3:248 (2004) FIG. 1
Biotrophic leaf-perforating parasite on *Frullania dilatata* (L.) Dumort.; Europe.

Ascospores dumbbell-shaped, rarely almost cylindrical, two-celled but seemingly one-celled, with a central cyanophilic band-like part, (6–)6.5–7.5(–8) \times 2–2.5 μm ; irregularly arranged in asci but generally orientated parallel to long axis of ascus, sometimes in pairs of two spores lying side by side (GERMANY, BAVARIA: Kohlgraben southwest of Dießen, 4 May 2003, P. Döbbeler 7741, M).

Bryocentria metzgeriae (Ade et Höhn.) Döbbeler,

Mycol Progr 3:252 (2004) FIG. 2
Necrotrophic leaf-perforating parasite on hepatics including *Frullania dilatata*; Europe.

Ascospores fusiform, two-celled but seemingly one-celled, with a central cyanophilic band-like part, (4.5–)5.5–7.5(–8.5) \times 1.5–2(–2.5) μm , irregularly ar-

ranged in asci but generally orientated parallel to long axis of ascus (GERMANY, BAVARIA: between St Ottilien and Türkenfeld, 1 May 1999, P. Döbbeler 7091, GZU).

Bryonectria callicarpa Döbbeler, Sendtnera 6:93

(1999) FIG. 3
Biotrophic parasite on the ventral side of *Frullania dilatata*; Europe.

Ascospores ellipsoid to fusiform, two-celled, not constricted at the septum, (11–)12–14(–15) \times 4–5 μm , colorless but with a large yellow lipid body in each cell and often an additional smaller one, epispor slightly cyanophilic (SPAIN: Catalonian Pyrenees, between Figueres and Olot, 20 Aug 1999, P. Döbbeler 7094, HOLOTYPE M).

***Bryonectria* sp.**

FIG. 4
Biotrophic parasite on *Frullania dilatata*; Romania.

Ascospores cylindrical to narrowly ellipsoid, two-septate, 18.5–23 \times 4.5–5 μm , epispor minutely rough and cyanophilic, 4 ascospores formed per ascus (ROMANIA: “Centralcarpathen, an den Stämmen der Nadelbäume” (without further details),

Kalchbrenner, Rabenhorst, Hep. Eur. 156, sub *F. dilatata*, HBG).

Calonectria frullaniae Racovitza, Mém Mus Natl Hist Nat, Sér B, Bot 10:28, 91 (1959) FIG. 5
Necrotrophic parasite within perianths of *Frullania dilatata*; Europe.

Ascospores cylindrical, straight or slightly bent, rounded at both ends, with up to seven transverse walls, $42\text{--}57 \times 2.5\text{--}3 \mu\text{m}$ (ITALY, TUSCANY: San Polo in Chianti, 6 Sep 2001, *P. Döbbeler* 7377, M).

Nectria brenesii Döbbeler et J. Carranza, Rev Biol Trop 41:203 (1993) FIG. 6
Biotrophic parasite on epiphyllous Lejeuneaceae; Costa Rica.

Ascospores bacilliform, bicellular when immature, at maturity disarticulating at the septum, part-ascospores one-celled, monomorphic, $(5\text{--})5.5\text{--}8\text{--}(9) \times (1.5\text{--})2\text{--}2.5 \mu\text{m}$ (COSTA RICA: Cordillera de Tilarán, Reserva Forestal de San Ramón, 21 May 1988, *P. Döbbeler* 6472, HOLOTYPE USJ).

Nectria byssophila Rossman, Mycotaxon 8:494 (1979) FIG. 7
Parasite on mosses (type, Sri Lanka [Ceylon]) and lichens (New Zealand).

Ascospores almost filiform, straight to slightly curved to sigmoid, parallel and twisted in the ascus, 9–17-septate, $125\text{--}240 \times 2\text{--}3 \mu\text{m}$, epispore smooth (SRI LANKA: Nuwara Eliya, 19 Jun 1927, *T. Petch*, HOLOTYPE K; description and illustration after Rossman 1983:74, FIG. 43).

Nectria contraria Döbbeler, Nova Hedwigia 66:354 (1998) FIG. 8
Parasite on epiphyllous *Radula flaccida* Lindenb. et Gottsche; Costa Rica.

Ascospores two-celled, one cell hemispherical, the other wedge-shaped, $(5.5\text{--})6\text{--}7 \times 2.5\text{--}3.5 \mu\text{m}$, epispore smooth, partly oriented with the hemispherical cell to the ascus tip, partly in the opposite direction to the ascus foot (COSTA RICA: CATIE near Turrialba, 24 Nov 1988, *P. Döbbeler* 6364, HOLOTYPE M).

Nectria foertheri Döbbeler, this publication FIG. 9

Nectria gynophila Döbbeler, Nova Hedwigia 66:358 (1998) FIG. 10
Parasite within perianths of epiphyllous *Radula flaccida* causing deformations; Costa Rica, Ivory Coast.

Ascospores spherical to broadly ellipsoid, often at one or both ends impressed and then almost cube-shaped, two-celled, $4\text{--}5\text{--}(5.5) \mu\text{m}$ diam, epispore smooth, cyanophilic (IVORY COAST: Parc National de Tai, 18 Dec 1975, *L. Aké Assi* 13160/A, HOLOTYPE EGR).

Nectria lagodes Döbbeler, this publication FIG. 11

Nectria lankesteri Döbbeler et J. Carranza, Rev Biol Trop 41:204 (1993) FIG. 12
Biotrophic parasite on epiphyllous Lejeuneaceae; Costa Rica.

Ascospores ellipsoid, two-celled, with thick walls and subglobose lumina, $5\text{--}6.5 \times 3.5\text{--}4.5\text{--}(5) \mu\text{m}$, epispore smooth or rough, slightly cyanophilic (COSTA RICA: Jardín Lankester southeast of Cartago, 11 Feb 1989, *P. Döbbeler* 6366, HOLOTYPE USJ).

Nectria muscivora (Berk. et Broome) Berk., Outl Brit Fung (London):394 (1860) FIG. 13
Necrotrophic parasite on acrocarpous mosses; Europe.

Ascospores ellipsoid to fusiform, two-celled, $(17\text{--})20\text{--}30\text{--}(32) \times (5.5\text{--})6\text{--}8\text{--}(8.5) \mu\text{m}$, bipolar asymmetrical, epispore cyanophilic, almost smooth or rough (GERMANY, NORTH RHINE-WESTPHALIA: Olpe, 9 Apr 2004, *P. Döbbeler* 7922, TUR).

Nectria sanramonensis Döbbeler, Brenesia 37:145 (1993) FIG. 14
Necrotrophic parasite on bryophytes; Costa Rica.

Ascospores narrowly ellipsoid, two-celled, with two oil-bodies per cell, $(13\text{--})16\text{--}19\text{--}(21) \times 5\text{--}6\text{--}(7) \mu\text{m}$, epispore with cyanophilic straight, coiled or slightly irregular lines in longitudinal direction (COSTA RICA: Cordillera de Tilarán, Reserva Forestal de San Ramón, 22 Mar 1991, *P. Döbbeler* 6509 et *R. Ortiz*, HOLOTYPE USJ).

Thyronectria hyperantarctica (D. Hawksw.) D. Hawksw. et Spooner in Pegler et al, Kew Bull 35: 519 (1980) FIG. 15
Parasite on mosses causing necrotic rings in moss carpets; South Orkney Islands, Antarctic Peninsula.

Ascospores cylindrical to clavate-cylindrical with broadly rounded ends, muriform, with 3–5 transverse septa and an irregular longitudinal septum running vertically or diagonally in most of these cells, $31\text{--}42 \times 13\text{--}20 \mu\text{m}$ (ANTARCTICA: Argentine Islands, Galindez Island, Meek Channel, 7 Mar 1965, *R.E. Longton* 2309, HOLOTYPE IMI; description and illustration

after Hawksworth 1973, Pegler et al 1980, Gamundi and Spinedi 1988).

Ticonectria perianthii Döbbeler, *Nova Hedwigia* 66: 362 (1998) FIG. 16

Parasite within perianths of epiphyllous *Radula flaccida*; Tropical America.

Ascospores ellipsoid to ovoid, two-celled, not constricted at the septum, $7-9(-10.5) \times 4-5(-6) \mu\text{m}$, epispore slightly rough and cyanophilic (COSTA RICA: CATIE near Turrialba, 24 Nov 1988, *P. Döbbeler* 6327, HOLOTYPE M).

Trichonectria hirta (A. Bloxam) Petch, *Naturalist (Hull)* 1937:282 (1937) FIG. 17

Parasite on lichens and mosses, also on wood and bark; Europe.

Ascospores cylindrical, often slightly tapering toward ends, 11–21-septate, sometimes slightly constricted at the septa, $(40-45-85(-95) \times 5-8(-9.5) \mu\text{m}$, epispore smooth (AUSTRIA, STYRIA: Koralpe, Oberlaufeneegg between Deutschlandsberg and Freiland, 8 Apr 1973, *J. Poelt*, GZU; description and illustration after Döbbeler 1978, Rossman et al 1999).

DISCUSSION

Ascospore types and features.—The hypocreaceous ascomycetes growing on mosses and hepatics exhibit a wide range of ascospore types (FIGS. 1–17). This heterogeneity is remarkable because the bryophilous species represent only a very small part of the more than 1000 species described within the Hypocreales (Rossman et al 1999:3).

Most frequent type of ascospore is didymosporous and this character predominates in Hypocreales. In *Bryocentria brongniartii* and *B. metzgeriae* ascospores are seemingly one-celled, but have a delicate, often invisible transverse septum. The dented ascospores of *Nectria gynophila* (also in *N. perianthicola* Döbbeler et J. Carranza on epiphyllous hepatics in Costa Rica, Döbbeler and Carranza 1993) have this form even when in a turgid state (i.e. they are not collapsed) as is common in ascospores that are ejected into the air (Read and Beckett 1996). *Nectria brenesii* is characterized by disarticulating ascospores, a feature that is widespread taxonomically (Peterson and Rikkinen 1998) and well known in the Hypocreales. *Nectria lagodes* has dimorphic cells and only the smaller cell has cytoplasm. This fertile cell ($2-3 \times 1 \mu\text{m}$) is smaller than many nectriaceous ascoconidia or microconidia (e.g. Booth 1959). Ascospores with bipolar asymmetry are oriented normally so that the broader end is oriented toward the ascus apex, possibly in-

creasing the distance of discharge and making dispersal more effective (Ingold 1954, 1971). In *Nectria contraria*, *N. foertheri* and *N. lagodes* some ascospores are oriented thus but others lie in the opposite direction. Size, ascospore wall thickness and presence or absence of oil droplets or cyanophilic structures (e.g. episporic lines in *N. sanramonensis* and tiny warts in *N. muscivora*) are additional varying characters. Ascospores may be arranged differently within an ascus (e.g. uniseriately in *N. gynophila* or in fascicles in *N. foertheri*). Most two-celled ascospores illustrated here are assigned to species of *Nectria*, by far the largest genus of bryophilous Hypocreales with no fewer than 19 species recorded. However deviating excipulum characters, such as tissue type, probably indicate that not all representatives are congeneric.

The phragmosporous type is well represented by the obligately bryophilous *Calonectria frullaniae*. *Trichonectria hirta* and *Nectria byssophila* with multi-septate ascospores are both facultative moss-parasites. Two-septate ascospores formed in four-spored asci occur in *Bryonectria* sp. and in two other muscicolous *Bryonectria* species (Döbbeler 1978, Döbbeler and Hertel 1984). *Thyronectria hyperantarctica* is the only species with ascospores of the dictyosporous type.

Hypocrealean parasites with one-celled ascospores are not yet known on mosses or hepatics. Also missing are species that have colored ascospores or produce ascoconidia in the ascus or centrum.

Correlations between ascospore types and ecological aspects.—Elucidating patterns of relationships between ascospore morphology and the ecological niches occupied by different ascomycetes has been attempted by relatively few authors (Poelt 1973, Sherwood 1981). Bryophilous ascomycetes are poorly known and interpretation of the adaptive significance of spore features is hindered by a lack of data on host ranges, ecology, frequency and geographical distribution. However one example regarding parasites on epiphyllous hepatics seems to indicate a general trend. All seven *Nectria* species recorded on epiphyllous Lejeuneaceae and *Radula flaccida* have small ascospores or part ascospores ($<10 \mu\text{m}$, four of them $<7 \mu\text{m}$ as the largest dimension) (Corner 1935, Döbbeler and Carranza 1993, Döbbeler 1998). They were collected mostly at elevations <1000 m. These parasites also have reduced ascomata. It is unclear whether the small size of the ascospores favors dispersal or reflects the environmental conditions in the phyllophaere of tropical low land rainforests. The great majority of epiphyllous hepatics are disposed among the Lejeuneaceae (Gradstein 1997), a group that represents the smallest hepatics known and which osten-

sibly would offer only a small amount of nutrients to support parasitic growth.

In tropical America Samuels (1997) observed that species with large ascospores tend to occur at elevations >1500 m, whereas species with smaller ascospores tend to be found at lower elevations. This agrees with observations on Xylariaceae made by Rogers (2000), who said that “where taxa are separable primarily on ascospore size, those with smaller spores are usually found in more tropical environments.”

Do differences in spore size within or between biotrophic and necrotrophic species have an adaptive value? Some observations may be relevant. Several necrotrophic species have small ascospores (<10 μm , e.g. *Bryocentria metzgeriae*, *Nectria lagodes*, *N. mnii* Döbbeler), whereas the necrotrophic *N. muscivora*, *N. racovitzae* Döbbeler, and *Thyronectria hyperantarctica* are large-spored (ascospores longer than 20 μm). In this instance infection potential differs because spore output from ascomata of equal size, differs significantly. On the other hand, necrotrophs may compensate by having a broader host range. *Bryocentria brongniartii* is a biotrophic parasite on *Frullania dilatata*, whereas the necrotrophic *B. metzgeriae* infects various thallose and foliose hepatics representing five families (Döbbeler 2004). Both species are found in the immediate vicinity of the same phorophyte and produce small ascospores (see above) of a comparable high number (<8000 per ascoma). The biotroph may stay indefinitely on the same host plants, but the necrotroph, which kills its host, compensates for being forced to change the substrate by having a wider taxonomic range of host plants.

How might ascospore heterogeneity be explained?—As shown previously a wide range of ascospore types exists in bryophilous Hypocreales, although the ecological conditions of the host plants may be similar or identical. Especially instructive is the ascospore heterogeneity of the six species known from corticolous *Frullania dilatata* (marked by an asterisk in Figs. 1–5, 11). Apart from *Bryocentria metzgeriae*, all are recorded exclusively on that host and occur, apart from *Bryonectria* sp., sympatrically in a small region of Tuscany, Italy. Are there any reasons that may explain this diversity? As with most bryophilous ascomycetes, the ascomata of hypocrealean parasites are tiny and hidden by the host leaves; it is almost impossible to detect them under field conditions in spite of their bright colors. Nearly all records are based on screening randomly gathered specimens with stereomicroscopic magnification. This means that the presence of a species is recorded by chance and records are not the result of a systematic inven-

tory related to hosts or areas. Therefore ascospore types could represent by chance the extremes of the variation range and further studies would perhaps reveal intermediate types. The many Hypocreales recorded so far on relatively few host species, the high percentage of species known only from very few or single collections and the many undescribed species observed indicate that only a small part of the hypocrealean diversity on bryophytes actually is known. However this assumption seems not to hold for fungi on *Frullania dilatata*, where there is a concentration of spore diversity. During the past two decades more than 300 European potential host specimens have been carefully analyzed, resulting in a good concept of the more common fungi present.

An alternative explanation may be derived from island biogeography. A typical phenomenon associated with oceanic islands is the unbalanced and disjoint composition of their plants and fungi in comparison to the continental regions from which diaspores presumably originate (Gradstein and Weber 1982 for bryophytes, Lücking and Kalb 2001 for lichens, Morat 1993 for angiosperms). In this sense host species or groups of related hosts may serve as islands for specific parasites. The host populations are surrounded and isolated by nonhosts or substrates unsuitable for colonization. The frullaniicolous *Calonectria frullaniae*, for example, does not grow on the bark of *Acer pseudoplatanus*, or on corticolous hepatics and mosses such as *Radula*, *Metzgeria*, *Porella* or *Leucodon*. *Calonectria frullaniae* depends on a single host species, *Frullania dilatata*, whether it is closely associated or even intermingled with other bryophytes or forms isolated mats on a phorophyte. Colonization of new hosts can be regarded as a result of a repetitive stochastic process where fungal species on soil, wood, bark or living or dead parts of plants evolved to infect ecologically associated bryophytes by adapting to the conditions of these new substrates and becoming specific. Hypocreales seem to be especially predisposed for such developments: They are rich in species which occur throughout the world on a vast range of hosts and habitats (Rossman 1996), including the most common fungi in certain tropical regions (Samuels and Dumont 1982, Samuels et al 1990).

Jumping to new hosts is much more common in rust and smut fungi than has been realized (Savile 1990) and there is no reason to assume that this phenomenon would not occur in bryophilous fungi. This would lead to a heterogeneous assemblage of parasitic ascomycetes, some of which would share bryophytes as hosts (bryophilous Hypocreales) and others which would be restricted, even to a single host species (Hypocreales on *Frullania dilatata*). This con-

cept implies that phylogenetic relationships often will be closer between bryophilous and nonbryophilous species than among purely bryophilous ones. However there is no doubt that adaptive radiation also plays an important role in the evolution of bryophily. The hypocrealean *Bryonectria* is an obligately bryophilous genus (i.e. its species are exclusively known from mosses and hepatics). Several undescribed species on epiphyllous Lejeuneaceae from rainforests in Costa Rica form a distinct assemblage well defined by morphological, anatomical and biological features such as hyaline, gelatinous perithecia, similar ascospores, superficial hyphae with lateral appressoria and symptomless infections (Döbbeler unpublished). Thus species diversity of fungal parasites on bryophytes, as expressed by ascospore heterogeneity, could be compared to patterns of colonization and adaptive radiation on islands, with the islands in this case being suitable host bryophytes. Questions arising from this hypothesis offer a wide field of future research by classical as well as modern methods.

DESCRIPTION OF TWO NEW SPECIES

Perithecia of *Nectria foertheri* and *N. lagodes* perforate the protecting host leaf from the ventral side, and form ostioles that open level with the free-lying, dorsal side (microniche 2.4.3. in Döbbeler 2002).

Nectria foertheri Döbbeler, sp. nov. FIGS. 18–27

Hyphae 1.5–3 μm latae, incoloratae, supra cellulas ventrales foliorum repentes. Perithecia folia perforantia, 150–210 μm diametentia, subglobosa, dilute flava, hyphis plus minusve densis obiecta. Ostiolum inconspicuum, perpusillum; canalis ostioli periphysibus repletus. Paries peritheciarum externe visus cellulis angulatis vel rotundis, 7–14 μm latis compositus, in sectione longitudinale lateraliter 13–20 μm crassus, e 4–6 stratis cellularum tangentialiter extensarum formatus; parietes cellularum cyanophili. Paraphyses apicales presentes. Asci unitunicati, 30–46 \times 4.5–5 μm , cylindrici vel subclaviformes, valde leptodermici, aparatu apicali carentes, copiosi, octo-sporei; reactio iodi negativa. Ascosporeae 20–24 \times 1.5–2 μm , anguste cylindricae, in parte centrali angustiores, versus ambas fines gradatim dilatatae, bicellulatae; cellula minoris 4–5.5 μm longa. Conidiomata vel conidia non visa. Habitat parasitice in foliis vivis hepaticae *Porella* sp.

Hyphae 1.5–3 μm wide, colorless, with ramifications and anastomoses, cyanophilic, growing superficially and irregularly over ventral leaf cells near perforation point and over stems; hyphae on dorsal side of perforated leaves missing; few hyphae within leaf cells surrounding the perforation sometimes present; hyphae of unknown affinity also within peripheral stem cells. *Perithecia* leaf-perforating, (130–)150–210(–240) μm diam, subglobose, apically flattened

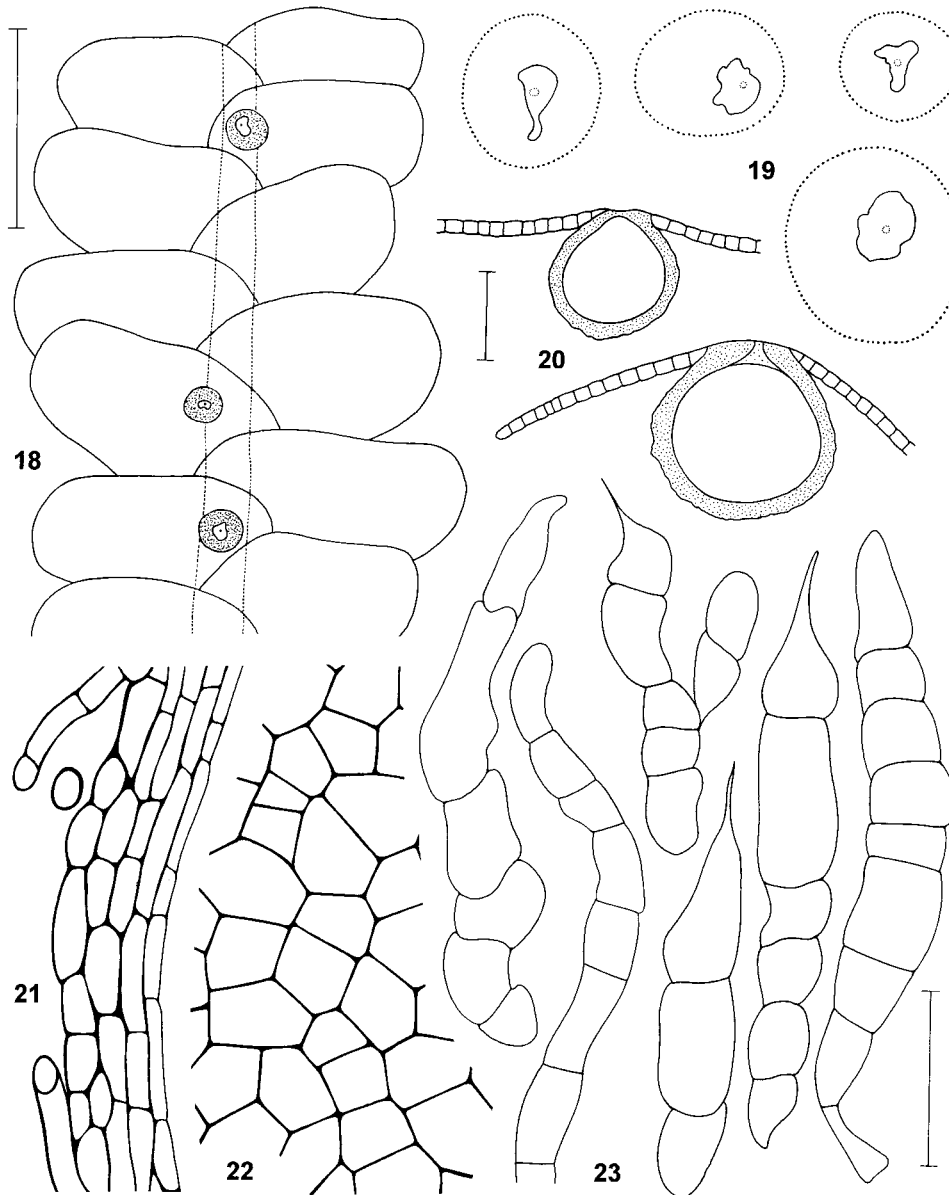
and forming at dorsal leaf level an irregular disk-like structure, 50–80 μm diam, yellowish to whitish; no color change in KOH; apically sometimes with few blunt setae up to 15 μm long and 3–6 μm wide at base, medium and lower part surrounded by loosely interwoven, adjacent, 2–3(–4) μm wide, colorless hyphae. *Ostiolum* inconspicuous, punctiform, ca. 15 μm diam, ostiolar canal lined with periphyses. *Excipulum* in medium and basal part with (5–)7–14(–17) μm wide, angular or slightly rounded cells with rather thin walls, cells apically smaller and with thicker walls; excipulum in longitudinal section (10–)13–20 μm wide, composed of 4–6 layers of tangentially stretched applanated cells, inner cells thin-walled and longer (–15 μm) than the thicker walled medium and outer cells; all excipular cells including setae and adjacent hyphae with cyanophilic walls; above hymenium a cushion of thin-walled, angular, noncyanophilic cells. *Apical paraphyses* between asci, very delicate, forming irregular, sparsely branched chains up to 50(–80) μm long, individual cells strongly varying in size, inflated, thin-walled, 6–15(–25) \times 4–10(–12) μm , distal cell sometimes collapsed. *Asci* unitunicate, 30–46(–55) \times 4.5–5(–6) μm , cylindrical or subclaviform, straight or slightly curved, thin-walled and often hardly visible, apically rounded and without internal structures, numerous, eight-spored; empty asci up to 105 μm long, often apically expanded; iodine (Lugol) reaction negative. *Ascospores* (18–)20–24(–26) \times 1.5–2 μm , narrowly cylindrical, narrowest in central part, toward both ends gradually enlarged and rounded, colorless, of two different cells, the smaller cell (3.5–)4–5.5(–6) μm long, the longer with little cytoplasm, its distal cell wall (in relation to smaller cell) with a cup-like, 1.5–3(–3.5) μm wide wall thickening; ascospores forming 25–35(–40) μm long and 5–7(–8) μm wide fascicles lying in upper part of asci; individual free lying spores rarely observed; orientation of spores within a fascicle varying, smaller cell partly oriented to ascus apex, partly to base. *Anamorph* not observed.

Specimen examined. GUATEMALA, ALTA VERAPAZ: Sierra de Chamá/Montaña Yalijux, mountain ridge north of the Finca Chelem-há, ca. 15 km air line northeast of Tucurú, between 15°23'22"N, 90°04'12"W and 15°23'05"N, 90°04'33"W, 2300–2400 m altitude, on *Porella* sp., terrestrial, primary cloud forest with *Quercus* and Myrtaceae, 9 Sep 1999, H. Förther s. n. (HOLOTYPE M).

Etymology. Named after Dr Harald Förther (München), who collected the species, along with several others, during one of his expeditions in Guatemala.

Distribution. Known only from the type collection.

Notes. *Nectria foertheri* obligately perforates host leaves. Perithecia occur sporadically in most cases on



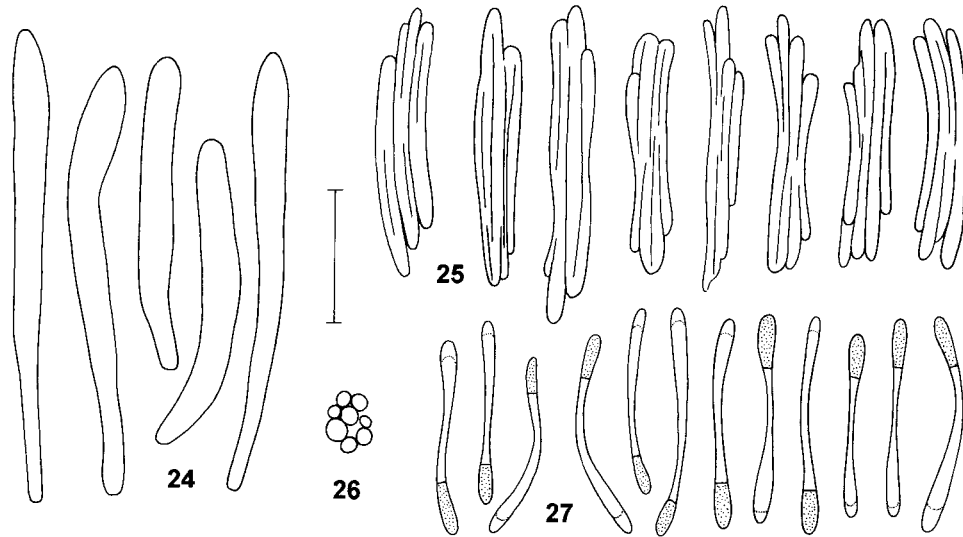
FIGS. 18–23. *Nectria foertheri* (holotype). 18. Part of a host plant with ascomata seen from above (dorsal view). Bar = 1 mm. 19. Ascomata in outline seen from above. 20. Ascomata perforating leaves in longitudinal section. FIGS. 19, 20 bar = 100 μm . 21. Ascomatal wall in longitudinal section. 22. Excipular cells seen from the outside. 23. Apical paraphyses. FIGS. 21–23 bar = 20 μm .

the lower leaves of a plant. They clearly prefer the proximal parts of individual leaves covering the stems. Apart from the small perforation point there is no visible damage. Host cells surrounding the perithecial disk even contain oil-bodies.

The species is characterized by its unique ascospore-type. However there are a few ascomata of an unnamed muscicolous *Nectria* from Florida at the Herbarium of the New York Botanical Garden that might be related: Perithecia superficially on the leaves, pyriform, up to 250 μm diam, setae up to 30

μm long and 3–6 μm wide, thick-walled, formed only in the apical part of the ascomata; excipulum covered by adjacent, colorless, thin-walled hyphae; asci cylindrical, about 5 μm wide; ascospores two-celled, 16–17 \times 1.5 μm , smaller cell 3–4 μm long, the longer cell appendage-like, with little cytoplasm, hyphae up to 3 μm wide, epi- and intracellular. Label data: USA, FLORIDA: West Palm Beach, near cemetery, on *Isopterygium tenerum* (Sw.) Mitt., 1897–1898, R. Thaxter (NY, vidi).

Both species have similar two-celled ascospores



FIGS. 24–27. *Nectria foertheri* (holotype). 24. Immature asci. 25. Ascospore fascicles. 26. Ascospore fascicle in transverse section. 27. Ascospores (small cell rich in plasmatic content stippled). FIGS. 24–27 bar = 15 μ m.

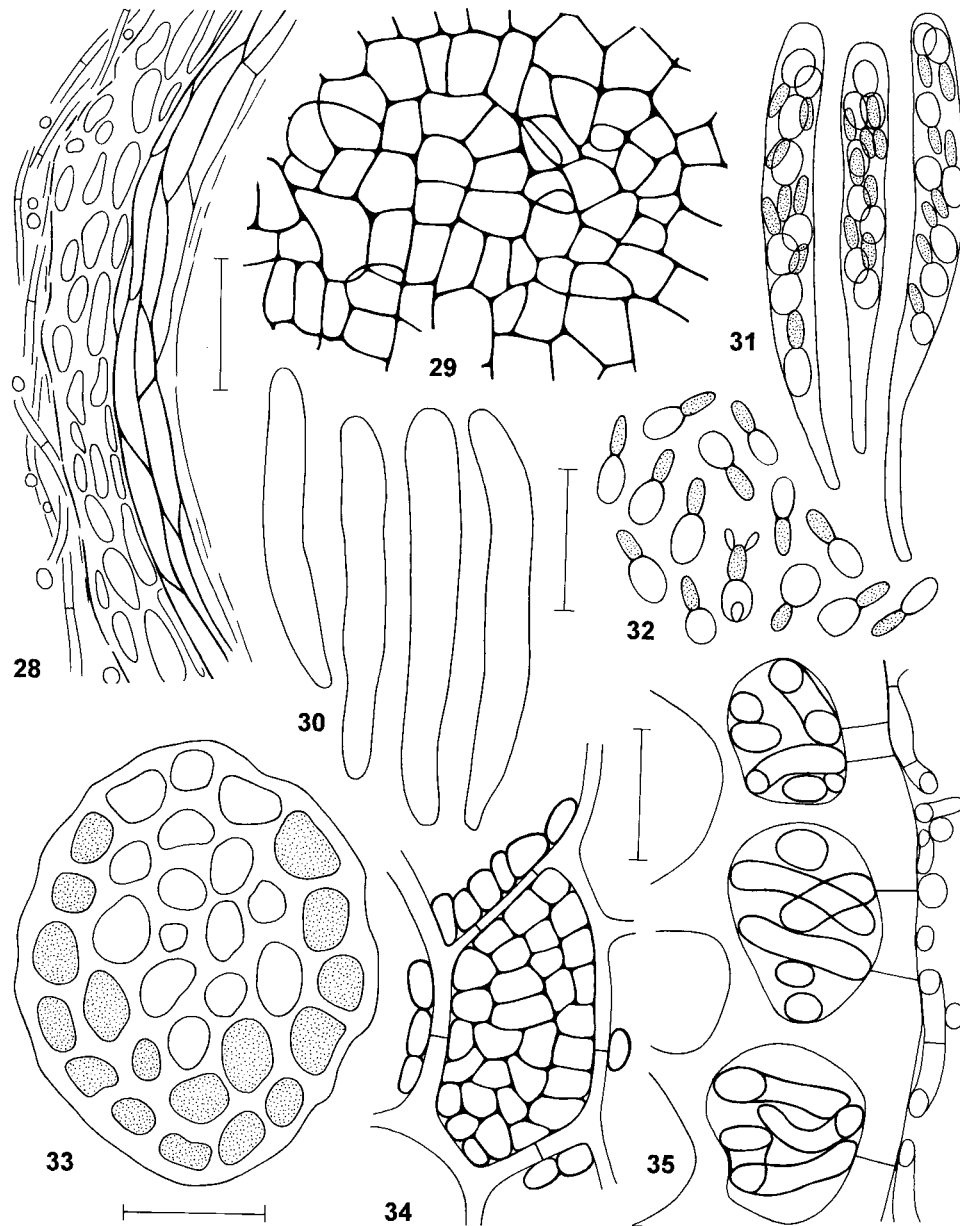
consisting of a small cell rich in cytoplasm and a longer, appendage-like cell with less cytoplasm. Whether these cells also differ functionally is not known.

***Nectria lagodes* Döbbeler, sp. nov.** FIGS. 28–35

Hyphae inter folia supra cellulas et intra cellulas hospitis crescentes; basi perithecorum mycelium blancum arachnoideum e hyphis 1.5–2 μ m latis formantes; hyphae intracellulares usque ad 5 μ m latae, dilute brunneolae. Perithecia folia perforantia, 170–250 \times 150–220 μ m, subglobosa vel pyriformia, aurantiaca, apicaliter interdum setis brevibus ornata, pars media et basalis perithecorum hyphis plus minusve densis oblecta; perithecia KOH non mutata. Ostiolum inconspicuum, perpusillum; canalis ostioli periphysibus repletus. Parietes perithecorum externe visus cellulis angulatis vel rotundis, 4–9 μ m latis compositus, in sectione longitudinale 12–18 μ m crassus, e stratis nonnullis cellularum tangentialiter extensarum formatus. Asci unitunicati, 25–40 \times 4–5 μ m, cylindrici, leptodermici, sine aparato apicali, copiosi, octo-sporei; reactio iodi negativa. Ascosporae 5–6 \times 2–3 μ m, incoloratae, cellulis duabus dissimilibus constantes, cellula minoris 2–3 \times 1 μ m, ellipsoidalis vel fere cylindrica, cellula maiora 3–4 \times 2–3 μ m, subglobosa vel late ellipsoidea. Conidiomata vel conidia non visa. Habitat parasitice in foliis emorientibus vel emortuis hepaticae *Frullania dilatata*.

Mycelium consisting of ramified and anastomosing hyphae between leaves and upon and within host cells; arachnoid white hyphae at base of perithecia and between leaves often visible by stereomicroscopic magnification (40 \times), 1.5–2(–3) μ m wide; hyphae upon leaf cells similar, forming irregular nets, many ramifications arising in right angles, haustoria not observed; intracellular hyphae within peripheral stem and basal leaf cells, (1–)2–4(–5) μ m wide, pale brownish, with thicker walls than the superficial hy-

phae, infected cells often completely occupied, hyphal cells then angular in outline by mutual pressure, 3–5(–6) μ m diam, hyphae growing from one host cell to another by delicate perforations crossing walls perpendicularly, intracellular hyphae connected to small-celled hyphal coverings upon stems by the same type of perforations; leaf cells adjacent to ascomatal perforation point without intracellular hyphae. *Perithecia* leaf-perforating, ca. 170–250 \times 150–220 μ m, subglobose to pyriform, apically flattened and sometimes with a few blunt setae up to 30(–40) μ m long and 2.5–4.5 μ m wide at base, orange-red; no color change in KOH; medium and lower part surrounded by loosely interwoven, adjacent, 1–2 μ m wide, colorless hyphae. *Ostiolum* inconspicuous, punctiform, ca. 5 μ m diam, ostiolar canal lined with periphyses. *Excipulum* in medium and basal part with 4–9(–12) μ m wide, angular or slightly rounded cells with rather thin cyanophilic walls, cells apically smaller and with thicker walls; excipulum in section 12–18(–20) μ m wide, composed of several layers of tangentially stretched flattened cells, inner cells thin-walled and longer (–15 μ m) than thick-walled outer cells. *Apical paraphyses* present. *Asci* unitunicate, 25–40(–50) \times (3.5–)4–5(–6) μ m, cylindrical, thin-walled, without apical structures, numerous, eight-spored; iodine (Lugol) reaction negative. *Ascospores* 5–6(–7) \times 2–3 μ m, colorless, of two different cells, smaller cell 2–3(–3.5) \times 1(–1.5) μ m, ellipsoid to almost cylindrical, with dense plasmatic content, larger cell 3–4 \times 2–3 μ m, subglobose to broadly ellipsoid, without plasmatic content, its distal wall region (in relation to smaller cell) often very delicate or even disappearing; orientation of spores within an ascus varying, smaller



FIGS. 28–35. *Nectria lagodes*. 28. Ascomatal wall in longitudinal section. 29. Excipular cells seen from the outside. FIGS. 28, 29 bar = 15 μm . 30. Immature asci. 31. Mature asci. 32. Ascospores (small cell rich in plasmatic content stippled). FIGS. 30–32 bar = 10 μm . 33. Stem of host plant in transverse section (cell colonized by hyphae stippled). Bar = 40 μm . 34. Hyphae occupying a stem cell. 35. Superficial hyphae penetrating the periclinal wall of the host stem forming an intracellular mycelium. FIGS. 34, 35 bar = 15 μm . FIGS. 28, 29, 31–35 holotype, FIG. 30 *G. et P. Döbbeler 4303*, M.

cells partly oriented to the apex, partly to the base. *Anamorph* not observed.

Etymology. *lagos* (Greek) = hare, *-odes* (Greek) indicates resemblance; FIG. 32.

Distribution. Italy, Greece.

Notes. The species grows necrotrophically on *Frustraria dilatata* with discolored spots within the host mats. Infected plants begin to die off. Ascomata develop most often protected between two overlapping leaves. Single perithecia also may be superficial and

found sporadically on any part of the plant including male inflorescences.

The aerial hyphae of *Nectria lagodes* may favor a rapid spreading of the fungus because they need not grow from cell to cell but have a certain independence from the host. Such a mycelium does not occur in all necrotrophic parasites on bryophytes but is typical for a few nectriaceous species and *Acrospermum adeanum* Höhn., where it forms a small whitish zone at the front of the infection. This is particularly

well developed under wet conditions, when the infection expands (Döbbeler 1979). In addition to the superficial hyphae, *N. lagodes* forms an elaborate mycelium of angular hyphal cells within the stem cells of the host.

A relationship may exist with *Bryocentria*, a hypocrealean genus comprising three bryophilous species with comparable hymenial features, such as small cylindrical, thin-walled, numerous asci, presence of apical paraphyses, very small ascospores and a similar excipular structure (Döbbeler 2004). The type of the genus, *B. brongniartii*, is a frequent biotrophic parasite of *Frullania dilatata* whereas *B. metzgeriae* grows necrotrophically on corticolous Jungermanniales including *F. dilatata*. Furthermore both species perforate host leaves like *Nectria lagodes* and occur in Europe. *Bryocentria* is mainly characterized by two-celled ascospores surrounded by a central cyanophilic band (FIGS. 1, 2).

Nectria lagodes seems to be a rare species. It is known only from two collections, although several hundred specimens of *Frullania*, especially *F. dilatata*, from Tuscany and other parts of Europe, have been screened. As with other necrotrophic parasites it hardly can be overlooked because the bleached infected host-mats are conspicuous.

Specimens examined. ITALY, TUSCANY, FIRENZE: Greve in Chianti, trees at the side of a street within the town, on *Frullania dilatata*, ca. 270 m altitude, 5 Sep 2001, P. Döbbeler 7562 (HOLOTYPE M). GREECE, PELOPONNESE, ACHAÏA: about 5 km before Káto Vlasía between Chalandrítsa and Kaláyríta, 2 Oct 1981, G. et P. Döbbeler 4303 (M, only mount).

The most striking feature of both new species are the one-septate ascospores with dimorphic cells. There is a small cell rich in cytoplasm and a larger one with less cytoplasm in *Nectria foertheri* or without visible cell contents and therefore presumably sterile in *N. lagodes*. If this interpretation is correct, *N. lagodes* exhibits dimorphic ascospore cells regarding form and function. Within the nectriaceous fungi, ascospore cell dimorphism also is known in the wood-inhabiting stromatic *Podostroma alutaceum* (Pers.:Fr.) G.F. Atk. (Hypocreaceae), whose one-septate, ascospores divide still within the asci into differently shaped part-ascospores. The distal cell is (sub-)globose, the proximal oblong to wedge-shaped. Apart from morphology, both cells appear similar (Rossman et al 1999).

The appropriate systematic position of the new species is difficult to ascertain. Key characters for distinguishing genera in the Hypocreales, such as presence or absence of stromata and formation of superficial or immersed ascomata, are not suitable. A re-

currence theme in the bryophilous habit are reductions resulting in tiny fruit bodies that a priori are poor in characters (Döbbeler 1997). Stromata do not occur presumably because the leaves of mosses and hepatics are too delicate to support such structures. The immersion of ascomata into the substrate is impossible because the leaves of bryophytes are only one cell layer thick. Conidial states have considerable taxonomic significance but these are missing in both new species, as they are in most bryophilous Hypocreales.

Neither species is closely related to *Nectria cinnabarina* (Tode:Fr.) Fr., the type species of *Nectria* (Nectriaceae), which differs mainly by having crowded ascomata on an erumpent stroma, a positive KOH reaction, ellipsoid ascospores of two almost equal cells and a *Tubercularia*-anamorph. An alternative placement of the new species in the Bionectriaceae, which do not react with KOH, probably would require erection of a new genus. The key and the descriptions for the 26 genera included in the Bionectriaceae (Rossman et al 1999) reveals that none of them is suitable. At the moment I therefore prefer to assign them to the genus *Nectria* Fr. in the traditional broad sense. A better disposition must await more comprehensive studies of the *Nectria*-like fungi on mosses and hepatics.

ACKNOWLEDGMENTS

I am indebted to Clark T. Rogerson and Gary J. Samuels for sending the Thaxter material many years ago. The manuscript was improved substantially by critical remarks of Brian Coppins and two anonymous reviewers.

LITERATURE CITED

- Booth C. 1959. Studies of Pyrenomycetes: IV. *Nectria* (Part I). Mycol Papers 73:1–115.
- Corner EJH. 1935. A *Nectria* parasitic on a liverwort: with further notes on *Neotiella crozalsiana*. Gard Bull Straits Settlement 8:135–144.
- Döbbeler P. 1978. Moosbewohnende Ascomyceten I. Die pyrenocarpen, den Gametophyten besiedelnden Arten. Mitt Bot Staatssamml München 14:1–360.
- , 1979. Moosbewohnende Ascomyceten II. *Acrospermum adeanum*. Mitt Bot Staatssamml München 15:175–191.
- , 1997. Biodiversity of bryophilous Ascomycetes. Biodiv Conserv 6:721–738.
- , 1998. Ascomyceten auf der epiphyllen *Radula flaccida* (Hepaticae). Nova Hedwigia 66:325–373.
- , 1999. Two new species of *Bryonectria* (Hypocreales, Ascomycetes) on bryophytes. Sendtnera 6:93–102.
- , 2002. Microniches occupied by bryophilous ascomycetes. Nova Hedwigia 75:275–306.

- , 2004. *Bryocentria* (Hypocreales), a new genus of bryophilous ascomycetes. *Mycol Progr* 3:247–256.
- , Carranza J. 1993. Cuatro especies nuevas de *Nectria* (Hypocreales: Ascomycetes) en hepáticas epífilas de Costa Rica. *Rev Biol Trop* 41:203–208.
- , Hertel H. 1984. Drei neue moosbewohnende Ascomyceten aus der Subantarktis (Marion Island). *Sydowia* 36(1983):33–45.
- Gamundí IJ, Spinedi HA. 1988. Ascomycotina from Antarctica. New species and interesting collections from Danco Coast, Antarctic Peninsula. *Mycotaxon* 33:467–482.
- Gradstein SR. 1997. The taxonomic diversity of epiphyllous bryophytes. *Abstracta Botanica* 21:15–19.
- Gradstein SR, Weber WA. 1982. The bryogeography of the Galapagos Islands. *J Hattori Bot Lab* 52:127–152.
- Hawksworth DL. 1973. *Thyronectria antarctica* (Speg.) Seeler var. *hyperantarctica* D. Hawksw. var. nov. *Bull Brit Antarc Surv* 32:51–53.
- Ingold CT. 1954. Ascospore form. *Trans Brit Mycol Soc* 37:19–21.
- , 1971. Fungal spores. Their liberation and dispersal. Oxford, Clarendon Press.
- Kirk PM, Cannon PF, David JC, Stalpers JA. 2001. *Ainsworth & Bisby's dictionary of the fungi*, 9th ed. Wallingford: CAB International.
- Kotlaba F, Pouzar Z. 1964. Preliminary results on the staining of spores and other structures of Homobasidiomycetes in cotton blue and its importance for taxonomy. *Feddes Repert* 69:131–142.
- Lücking R, Kalb K. 2001. New Caledonia, foliicolous lichens and island biogeography. *Bibl Lichenol* 78:247–273.
- Morat P. 1993. Our knowledge of the flora of New Caledonia: endemism and diversity in relation to vegetation types and substrates. *Biodiversity Letters* 1:72–81.
- Pegler DN, Spooner BM, Lewis Smith RI. 1980. Higher fungi of Antarctica, the subantarctic zone and Falkland Islands. *Kew Bull* 35:499–562.
- Peterson EB, Rikkinen J. 1998. *Stenocybe fragmenta*, a new species of Mycocaliciaceae with fragmenting spores. *Mycologia* 90:1087–1090.
- Poelt J. 1973. Systematic evaluation of morphological characters. In: Ahmadjian V, Hale ME, eds. *The lichens*. New York and London, Academic Press. p 91–115.
- Racovitza A. 1959. Étude systématique et biologique des champignons bryophiles. *Mém Mus Natl Hist Nat, Sér B, Bot* 10 (fasc 1):1–288; Pl. 1–84.
- Rambold G. 1995. Observations on hyphal, ascus and ascospore wall characters in Lecanorales s.l. *Crypt Bot* 5:111–119.
- Read ND, Beckett A. 1996. Ascus and ascospore morphogenesis. *Mycol Res* 100:1281–1314.
- Rogers JD. 2000. Thoughts and musings on tropical Xylariaceae. *Mycol Res* 104:1412–1420.
- Rossmann AY. 1983. The phragmosporous species of *Nectria* and related genera (*Calonectria*, *Ophionectria*, *Paranectria*, *Scoleconectria* and *Trichonectria*). *Mycol Papers* 150:1–164.
- Rossmann AY. 1996. Morphological and molecular perspectives on systematics of the Hypocreales. *Mycologia* 88:1–19.
- , Samuels GJ, Rogerson CT, Lowen R. 1999. Genera of Bionectriaceae, Hypocreaceae and Nectriaceae (Hypocreales, Ascomycetes). *Stud Mycol* 42:1–248.
- Samuels GJ. 1997. Tropical Hypocreales. In: Hyde KD, ed. *Biodiversity of tropical microfungi*. Hong Kong University Press. p 297–325.
- , Doi Y, Rogerson CT. 1990. Hypocreales. In: Samuels GJ, ed. *Contributions toward a mycobiota of Indonesia*. *Mem New York Bot Gard* 59:6–108.
- , Dumont KP. 1982. The genus *Nectria* (Hypocreaceae) in Panama. *Caldasia* 13:379–423.
- Savile DBO. 1990. Coevolution of Uredinales and Ustilaginales with vascular plants. *Rep Tottori Mycol Inst* 28:15–24.
- Sherwood MA. 1981. Convergent evolution in discomycetes from bark and wood. *Bot J Linnean Soc* 82:15–34.
- von Höhnelt F. 1919. Mykologische Fragmente. *Ann Mycol* 17:114–133.