Hypocrealean hyperepiphyllous ascomycetes

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Abstract: The phyllosphere of vascular plants in tropical rainforests is dominated by small mosses and especially liverworts that provide a substrate for many fruit-body forming fungal parasites. The Hypocreales (Sordariomycetes) are by far the most species-rich group within the Ascomycota. With currently 24 species from six genera they represent about two thirds of all known ascomycetes on epiphyllous bryophytes. These species are synoptically treated here, presenting relevant systematic and biological information. The following seven species are described as new: *Bryocentria phaeocarpa*, *Bryonectria calopoda, B. clandestina, B. cyclopoda, B. diplopoda, B. lobopoda,* and *Ticonectria capta. Nectria egens* is combined to *Bryonectria, N. gynophila* and *N. perianthiicola* to *Bryocentria.* There is an amazing array of morphological features including hyphal appendages, various types of parasitism including gall formation, selection of hosts, microniches and geographical distribution. The diversity is emphasized by a number of spore types not known in other ascomycetes. Almost all observed species grow on liverworts like *Radula* (Radulaceae) or Lejeuneaceae. Only one species infects the moss *Ephemeropsis tjibodensis*. With 18 species the New World tropics are much better represented than the Old World tropics with only seven species (one of them of Afro-American distribution). No less than 17 species occur in Costa Rica. Nine species are only known from their type collection.

The hyperepiphyllous species form an essential part of the mini-ecosystem on the surface of living leaves, enriching the complexity of the phyllosphere. Necrotrophic parasites contribute to dynamic processes whilst perianthicolous species reduce the fertility of their hosts. The ascomycetes of epiphyllous bryophytes have to cope – like their hosts – with an ephemeral and nutrient-poor substrate. The formation of tiny ascomata in low densities may be regarded as an adaptation to this unique substrate.

Key words: *Anthonectria, Bryocentria, Bryonectria, Gynonectria, Nectria, Ticonectria*, Hypocreales, Nectriaceae, Bionectriaceae, epiphyllous fungi, hepaticolous, bryophilous, perianthicolous species, phyllosphere.

1. Introduction

One of the most exciting features in tropical rainforests is the occurrence of mosses and liverworts that colonize the surface of living leaves of ferns and seed plants (Herzog 1926, Richards 1981, Vareschi 1980, Pócs 1982, Gradstein & Pócs 1989, Gradstein 1995, Lücking 1995). Epiphyllous bryophytes have always had a special fascination for ecologists and bryologists (Richards 1984). Most species belong to hepatics like the Radulaceae (Radulales) and especially the Lejeuneaceae (Porellales) (Gradstein 1994, 1997, Pócs 1996), whereas only very few mosses regularly grow on leaf surfaces. Together with foliicolous lichens bryophytes dominate the phyllosphere but cyanobacteria, algae and non-lichenized fungi, myxomycetes and small animals like nematodes, mites and insects, and even tiny vascular plants may also be present. These communities form "a microcosm – a complete ecosystem in miniature"

(Richards 1984) that is well-adapted to the special conditions of a nutrient-poor habitat in a constantly warm and humid climate.

Numerous studies deal with systematic and biological aspects of epiphyllous organisms (Frahm et al. 2003). However, primary leaf epiphytes are not always recognized as a potential nutritional source for fruit-body forming parasitic fungi. About 80 lichenicolous fungi are known to grow on many of the more than 800 foliicolous lichens (Matzer 1996, 1997, Lücking 2001, 2008). Numerous species infect non-lichenized leaf-inhabiting ascomycetes (Hansford 1946, Pirozynski 1977, Hughes 1993, Gams et al. 2004). Liverworts form the substrate for a growing number of obligately hyperepiphyllous fungi, a highly diverse group of ascomycetes. Up until the 1990´s bryophilous phyllosphere parasites were completely unknown, apart from *Nectria egens* described by Corner in 1935. This neglect is hard to understand considering that some of them have quite distinctive red or black fruit-bodies that stand out from the pale green colour of their hosts. These fungi substantially increase the complexity of the phyllosphere, interacting with their host plants as necrotrophic, biotrophic or even gall-inducing parasites. Several species selectively attack the developing sporophytes, preventing their maturation.

The phyllosphere is an ephemeral habitat because the life-span of the phorophyte leaves is limited. Richards (1984) regards epiphyllous bryophytes as the "biological nomads" of the forest. The time required for spores to go from one generation to the next may take less than a year (Schuster 1988). The epiphyllae show neotenic tendencies to shorten their life-cycle (Thiers 1988, Schuster 1991, Gradstein 1997, Gradstein et al. 2006). Successful parasites have to cope with the same conditions as their hosts, resulting in minute and often simply constructed fruit-bodies and thin-walled, colourless ascospores. Several species of hyperepiphyllous fungi exhibit a number of exciting features regarding ascospore types and hyphal appendages (Figs 5–10 for *Bryonectria* species) not known elsewhere in bryophilous or non-bryophilous ascomycetes.

Currently, more than thirty species of hyperepiphyllous fungi belonging to several classes of ascomycetes are recognized, which probably represent only a small fraction of the existing diversity. Judging from species number and frequency, one clade seems to be especially well suited to living on phyllosphere liverworts, the Hypocreales (Sordariomycetes, Ascomycotina). They comprise about two thirds of all hyperepiphyllous species recorded so far. The following overview of the hyperepiphyllous Hypocreales is a compilation of published and new information about their morphology, habits and habitats and describes seven novel species.

2. Materials and methods

In most cases, the ascomata of hyperepiphyllous ascomycetes will not be observed in the field, even if collecting conditions are good. When gathering phorophyte leaves for this purpose, leaves with a well-developed layer of epiphylls should be selected. Generally, young leaves with incipient bryophyte colonization are not a promising substrate. The principally two-dimensional liverwort layer is comparatively easy to survey using stereo-microscopic magnification (40×).

Before studying herbarium material, both the epiphyllous hepatic layer and the phorophyte leaf should be thoroughly wetted. Excess water should be soaked up to avoid inconvenient light reflections. Orange or red ascomata of hypocrealean parasites tend to lose their vivid colour in the dry state, rapidly becoming inconspicuous, and are sometimes extremely difficult to detect. It is therefore advantageous to investigate recently collected fresh specimens, which also facilitates the distinction between biotrophic and necrotrophic parasites. The margins of the ventral leaf sides and the perianths merit special attention because several species are restricted to these microsites. Hyaline perithecia hidden between the host leaves, like those of *Bryonectria*, are most difficult to detect. They tend to assume the same colour as the surrounding substrate and seem to disappear completely, depending on the angle of the incident light when leaves are moved by tweezers. It is a common experience to see transparent perithecia under transmitted light using microscopic magnification (100×) that were not observed on the same shoot using the stereo-microscope with incident light. Fruit-bodies can easily be confused with air bubbles, pollen grains, colonies of cyanobacteria or algae, developmental stages and faeces of small animals like insects and all kinds of detritus. Even structures like the gemmae of liverworts or empty capsules hanging out of the perianths may appear deceptively similar to fungal ascomata.

The sporadic occurrence and island-like infections mean that making vouchers is time-consuming. In order to (re)-locate infected hepatics, parts of the phorophyte leaf where ascomata concentrate were usually excised from the phorophyte leaf and preserved in individual envelopes. A number of vouchers consist of just a few perithecia, or even an illustration documenting the record.

The studies largely rely on herbarium material, often collected years ago. Lactophenol-cottonblue (CB) is indispensible for the differentiation of delicate structures like colourless hyphae and their appendages from the host cells. Additionally, cyanophilous reactions of epispore structures become visible. With the exception of the ascomata, all measurements and illustrations of hymenial elements and mycelial characters were made in mounts treated with CB. Extreme values are given in brackets. Delicate structures like apical paraphyses, (empty) asci, and certain ascospore and hyphal features are often best observed using CB and phase-contrast optics. The descriptions may slightly

deviate from earlier versions due to new results. All published illustrations are indicated. In many cases the host species have not been identified. Lejeuneaceae are "notorious" for being very difficult to identify (Gradstein 1997) and epiphyllous liverworts often grow densely intermingled forming an "Epiphyllendschungel" (Herzog 1926).

3. Synoptic key to the species of hyperepiphyllous Hypocreales

1. *Anthonectria mammispora*
2. *Bryocentria aequinoctialis*
3. *Bryocentria gynophila*
4. *Bryocentria manubriata*
5. *Bryocentria merospora*
6. *Bryocentria perianthiicola*
7. *Bryocentria phaeocarpa*
8. *Bryonectria calopoda*
9. *Bryonectria clandestina*
10. *Bryonectria cyclopoda*
11. *Bryonectria diplopoda*
12. *Bryonectria egens*
13. *Bryonectria lobopoda*
14. *Bryonectria protonematis*
15. *Bryonectria* sp.
16. *Gynonectria intraspora*
17. *Nectria brenesii*
18. *Nectria contraria*
19. *Nectria hyperepiphylla*
20. *Nectria lankesteri*
21. *Nectria turrialbae*
22. *Ticonectria capta*
23. *Ticonectria perianthii*
24. *Ticonectria testudinea*

Perithecium colour

Red	12
Light or dark brown	7, 22–24
Yellow, orange, ochre	1–3, 5, 6, 8, 16, 20, 21
Colourless, hyaline	4, 9–11, 13–15, 17–19

Perithecium length

Less than 100 µm	9, 13, 15
100–150 µm	2, 3, 5, 7, 8, 10–13, 15, 18–21
150–200 µm	4–7, 14, 17, 19, 20, 22, 23
200–300 µm	1, 6, 14, 16, 22–24
More than 300 µm	14, 16

Setae

Missing	1–7, 9–16, 22–24
Very short and mostly less than 30 µm long	2, 4, 5, 8, 10, 11, 17–21

Ascospores, number of cells

One or two	16
Two	1–4, 6-8, 10–15, 17–24
Three	5, 9

Ascospore length

Less than 7 µm	1–3, 5–7, 17–21
7 to 10 µm	1, 4, 7, 12, 15, 17, 22, 23
10–14 µm	8–15, 24
More than 25 µm	16

Ascospore number per ascus

Four	9, 19, 22
Three to eight	16
Eight	1–4, 6–8, 10–15, 18, 20, 21, 23, 24
Sixteen (by disarticulation of eight)	5, 17

Ascospores, special features

None	4, 8–15, 19, 21–23
Disarticulating spores	5, 17
Cells strongly dissimilar	1, 18, 24
With cyanophilous band	2, 3, 6, 7
Indented spores	3, 6
Thick-walled spores	20
Spores within spores	16

Appressoria, number of cells

Missing	1–7, 16, 17, 20–24
One-celled	9, 12, 14, 15, 18, 19
Two-celled	11, 13, 19
Three- or more celled	8, 10, 13

Haustoria

Within leaf cells	18, 19, 21
None	1–17, 20, 22–24

Anamorphs

Not recorded	2–5, 7, 8, 13–15, 17–22, 24
Single, conidiogenous cells	9, 10, 12
Conidiomata	1, 6, 11, 16, 23

Hosts

Ephemeropsis tjibodensis	14
Radula flaccida, *Radula* sp.	3, 7, 13, 15, 18, 22, 23
Lejeuneaceae	1, 2, 4–6, 8–12, 16, 17, 19–21, 24

Type of parasitism

Biotrophic	8–15, 17–21
Necrotrophic	2, 4, 5, 7
Bio-/necrotrophic (in perianthicolous species)	1, 3, 6, 16, 22–24
Gall-inducing	3, 22, 23

Microniches

Leaf-perforating	5, 7
Ventral leaf margin	8–10, 13, 15, 19
Perianthicolous	1, 3, 6, 16, 22–24
On and between the leaves (or protonemal filaments)	2, 4, 11, 12, 14, 17, 18, 20, 21

4. Hypocreoid ascomycetes

Several ascomycetes on epiphyllous liverworts closely resemble Hypocreales, but have a quite different systematic placement. The following hypocreoid taxa have repeatedly been observed:

Epibryon deceptor Döbbeler (Chaetothyriales) on *Radula flaccida* forms globose, hyaline ascomata up to 85 µm in size on the ventral leaf margin. The hymenial jelly becomes reddish in iodine. The ellipsoidal ascospores have five transverse septa (Döbbeler 1998, Döbbeler & Hertel 2013, distribution map).

Psoroglaena hepaticicola (Döbbeler & Vězda) H.Harada (Verrucariales) has ascomata with short setae arranged in a circular collar. The ascospores are subfusiform, 3-septate and 14–18 µm long. The hymenial jelly becomes reddish in iodine and the thallus is granular and inconspicuous. The lichen is recorded several times on *Radula flaccida* in Africa (Döbbeler & Vězda 1982, Döbbeler 1998).

Octosporella (Pezizales), with two described species, has yellowish perithecia-like ascomata with conspicuous setae, filiform paraphyses and one-celled, globose or ellipsoidal ascospores (Döbbeler & Menjívar 1992, Döbbeler 2011a).

Tubeufiaceae (Tubeufiales, see Boonmee et al. 2014) deviate from hypocrealean species by having bitunicate asci and usually fusiform to filiform,

transversely septate ascospores. So far, no bryophilous species have been described.

5. The hypocrealean species in alphabetical order

Bryophilous ascomycetes prefer or exclusively occupy certain microniches of the host plant for fruit-body formation (Döbbeler 2002). In most cases the hyperepiphyllous species develop their ascomata superficially on the dorsal leaf surface, although sometimes they can be more or less hidden between the leaves or shoots. Some species prefer the protected ventral leaf margin. Their perithecia adhere laterally and may protrude somewhat into the open air. Two species colonize the ventral leaf side and perforate the leaves with their apices. The leaves often bulge at the perforation point. The ostioles are level with the dorsal leaf surface or may protrude a little. The perianthicolous species remain completely confined to the interior of the perianths, apart from the conidiomata, which may develop between the leaves at the perianth base. When mature, the perithecia either perforate the perianth wall or use the natural apical opening for spore dispersal. These parasites behave biotrophically against the gametophyte, i.e. the foliose shoot of the liverwort, and necrotrophically against the sporophyte, whose structure becomes degraded.

Tab. 1: Presence or absence of anamorphs, hosts, types of parasitism, microniches occupied, and known geographical distributions of bryophilous hypocrealean ascomycetes.

Species	**Anamorphs**	**Hosts**	**Biology**	**Microniches**	**Known distribution**
Anthonectria mammispora	pulvinate conidiomata	*Drepanolejeunea* sp., Lejeuneaceae, sp. indet.	biotrophic on gametophyte, necrotrophic on sporophyte	perianthicolous	Costa Rica, French Guiana
Bryocentria aequinoctialis	not observed	Lejeuneaceae, sp. indet.	necrotrophic	on the leaves	Costa Rica, French Guiana
Bryocentria gynophila	not observed	*Radula flaccida*	biotrophic on gametophyte, necrotrophic on sporophyte; gall-inducing	perianthicolous	Honduras, Costa Rica, Ivory Coast, Uganda, D. R. Congo
Bryocentria manubriata	not observed	Lejeuneaceae, sp. indet.	necrotrophic	on and between the leaves	Costa Rica

Species	Anamorphs	Hosts	Biology	Microniches	Known distribution
Bryocentria merospora	not observed	Lejeuneaceae, sp. indet.	necrotrophic	leaf-perforating	Costa Rica, French Guiana
Bryocentria perianthiicola	pulvinate conidiomata	*Taxilejeunea* sp.	biotrophic on gametophyte, necrotrophic on sporophyte	perianthicolous	Costa Rica
Bryocentria phaeocarpa	not observed	*Radula flaccida*	necrotrophic	leaf-perforating	Madagascar, Tanzania
Bryonectria calopoda	not observed	Lejeuneaceae, sp. indet.	biotrophic	ventral leaf margin	Costa Rica; only type collection
Bryonectria clandestina	conidiogenous cells at hyphae	*Cyclolejeunea convexistipa, C. peruviana,* Lejeuneaceae, sp. indet.	biotrophic	ventral leaf margin	Costa Rica, Ecuador
Bryonectria cyclopoda	conidiogenous cells at hyphae	*Cyclolejeunea peruviana*	biotrophic	ventral leaf margin	Costa Rica
Bryonectria diplopoda	cushion-shaped conidiomata	Lejeuneaceae, sp. indet.	biotrophic	on and between the leaves	Colombia; only type collection
Bryonectria egens	conidiogenous cells at hyphae	*Leptolejeunea vitrea*	biotrophic	on and between the leaves	Malaysia (Pahang); only type locality
Bryonectria lobopoda	not observed	*Radula flaccida*	biotrophic	ventral leaf margin	Costa Rica; only type collection
Bryonectria protonematis	not observed	*Ephemeropsis tjibodensis*	biotrophic	on and between the protonemal filaments	Indonesia (Sumatra, Java), Philippines (Mindanao), Papua New Guinea
***Bryonectria* sp.**	not observed	*Radula flaccida*	biotrophic	ventral leaf margin	Tanzania, only one collection
Gynonectria intraspora	pulvinate conidiomata	*Odontolejeunea* sp.	biotrophic on gametophyte, necrotrophic on sporophyte	perianthicolous	Costa Rica, Panama
Nectria brenesii	not observed	Lejeuneaceae, sp. indet.	biotrophic	between the leaves	Costa Rica; only type collection

Species	Anamorphs	Hosts	Biology	Microniches	Known distribution
Nectria contraria	not observed	*Radula flaccida*	biotrophic	on and between the leaves	Costa Rica; only type collection
Nectria hyperepiphylla	not observed	Lejeuneaceae, sp. indet.	biotrophic	ventral leaf margin	New Caledonia; only type collection
Nectria lankesteri	not observed	Lejeuneaceae, sp. indet.	biotrophic	between the leaves	Costa Rica; only type collection
Nectria turrialbae	not observed	Lejeuneaceae, sp. indet.	biotrophic	on and between the leaves	Costa Rica; only type collection
Ticonectria capta	not observed	*Radula* sp. (sect. *Epiphyllae*)	biotrophic on gametophyte, necrotrophic on sporophyte; gall-inducing	perianthicolous	Indonesia (Java)
Ticonectria perianthii	pulvinate conidiomata	*Radula flaccida*	biotrophic on gametophyte, necrotrophic on sporophyte; gall-inducing	perianthicolous	Honduras, Costa Rica, Surinam, French Guiana
Ticonectria testudinea	not observed	*Cyclolejeunea convexistipa*	biotrophic on gametophyte, necrotrophic on sporophyte	perianthicolous	Costa Rica

1. *Anthonectria mammispora* Döbbeler, Mycologia 102: 405 (2010)

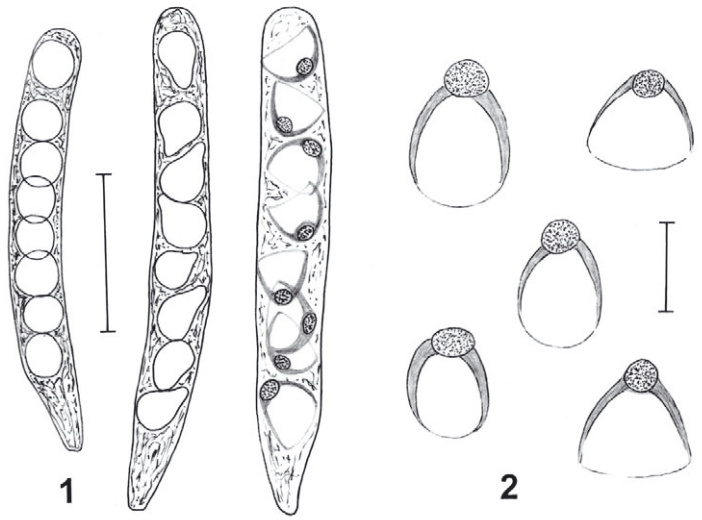

Fig. 1: *Anthonectria mammispora* (P. Döbbeler 8903). 1.1 Asci, the right one almost mature. Scale bar = 15 µm. 1.2 Ascospores, fertile cell stippled. Scale bar = 5 µm.

Type: Costa Rica, Prov. Alajuela: Southern surroundings of the volcano Arenal, Parque Nacional Arenal, 600 m, on *Drepanolejeunea* sp., 11 Mar 2008, P. Döbbeler 8647 (holotype USJ, isotype M).

Perithecia single within the distal part of the perianth, globose or pyriform, pale to golden-yellow or orange, without setae, 200–300 × 150–240 µm. Asci 30–50(–55) × 7–9(–10) µm, (6–, 7–)8-spored. Ascospores colourless, composed of 2 parts, fertile cell ellipsoidal to subglobose, (2–)2.5–4(–4.5) µm diam., sterile cell semiglobose to rarely globose, umbrella-like or lunate, optically empty, 6–9 µm diam. Conidiomata in leaf axils near the perianth, pulvinate, 25 µm high, conidiogenous cells cylindrical, 6 × 1.5 µm; conidia globose, colourless, 1–1.5 µm diam. (Döbbeler 2010a, Figs 1–9).

Hosts: *Drepanolejeunea* sp., Lejeuneaceae, sp. indet.

Known geographical distribution: Costa Rica, French Guiana.

Additional specimen examined: French Guiana: Matoury, Roura, route to Kaw (D6), Sentiel Botanique, 04°30’ N, 52°10’ W, 100 m, on Lejeuneaceae, 25 July 2009, L. Beenken (P. Döbbeler 8903 in M, only illustration).

2. *Bryocentria aequinoctialis* Döbbeler, Karstenia 50: 13 (2010)

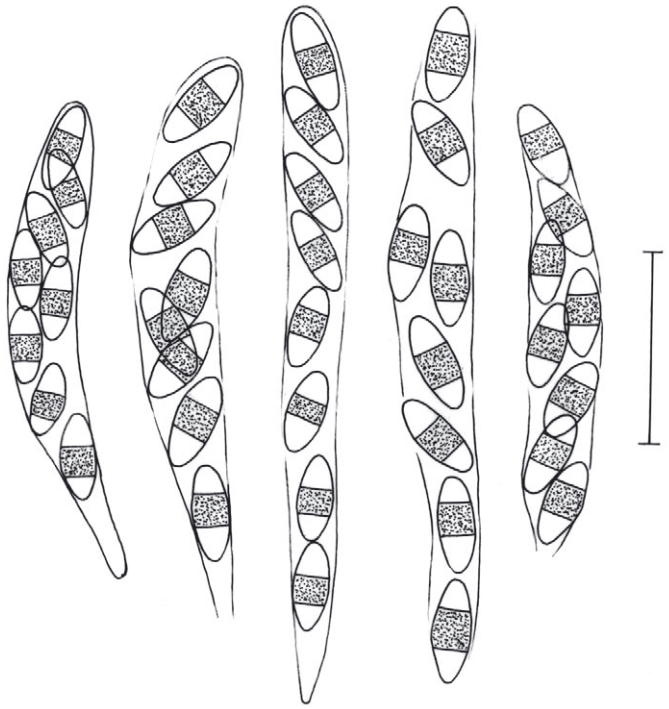

Fig. 2: *Bryocentria aequinoctialis* (P. Döbbeler 8899). Asci. Scale bar = 10 µm.

Type: Costa Rica, Prov. Alajuela: Surroundings of the volcano Arenal, east of the Laguna de Arenal, ca. 500 m, 2 Mar 2007, P. Döbbeler 8640 (holotype USJ).

Perithecia on the host leaves, subglobose to ovoid or conical, yellow to orange, without or with few setae near ostiole, (80–)110–150(–170) µm diam. Excipular cells 3–9(–12) µm with cyanophilous walls; surface loosely covered by adjacent hyphae. Asci (17–)20–33(–37) × (3.5–)4–5(–6) µm, 8-spored. Ascospores fusiform to ellipsoidal, 1-septate, colourless, (4–)4.5–6(–6.5) × (2–)2.5 (–3) µm, with a strong cyanophilous, central band obscuring the septum (Döbbeler 2010b, Fig. 1: a–d).

Host: Lejeuneaceae, sp. indet.

Known geographical distribution: Costa Rica, French Guiana.

Additional specimens examined: French Guiana: Matoury, Massiv de Mirande, 04°52' N, 52°21' W, 50 m, 15 July 2009, L. Beenken (P. Döbbeler 8898 in M). Kourou, Montange de Singes, 05°04' N, 52°42' W, 50 m, 17 July 2009, L. Beenken (P. Döbbeler 8899 in M, only 1 ascoma and illustration).

3. *Bryocentria gynophila* (Döbbeler) Döbbeler, comb. nov.

Basionym: *Nectria gynophila* Döbbeler, Nova Hedwigia 66: 358 (1998).

MycoBank: MB 814653

Type: Ivory Coast, Soubré: Parc National de Tai, 18 Dec 1975, L. Aké Assi 13160/A (holotype EGR).

Perithecia perianth-inhabiting, globose to pyriform, yellowish, without setae, 100–150(–160) µm diam. Excipulum densely covered with irregular hyphae. Asci 25–35 × 4–5 µm, 8-spored, numerous. Ascospores globose to broadly ellipsoidal, often depressed at one or both ends (even when turgid) and then almost cube-shaped, 1-septate, colourless, (3–)3.5–5(–5.5) µm in greatest diam.; epispore slightly cyanophilous; spores with a central, more strongly cyanophilous band-like part. Hyphae superficial on the inner perianth side and intercellular within the stems below the archegonia, partly with tiny, lobed cells (Döbbeler 1998, Fig. 15: 1, 2, Fig. 16: 1–7 Fig. 17: 1–3; 2010a, Figs 10–12).

Host: *Radula flaccida* Lindenb. & Gottsche.

Known geographical distribution: Honduras, Costa Rica. – Ivory Coast, Uganda, D.R. Congo.

Remarks: Up to six perithecia develop within the middle and upper part of a single perianth and perforate its wall. Infection may considerably alter the perianth's shape, resulting in cup-like, laterally compressed structures, apically up to 100 µm wide. Occasionally, perithecia were found to perforate vegetative host leaves from the ventral side closely situated to infected perianths. Stems below the perianths are sometimes considerably engorged by strongly developed internal hyphae, which may be regarded as a huge haustorium. In other cases, infected perianths look unaltered. However, regardless of external presentation, infection always prevents sporophyte maturation.

So far, *Bryocentria gynophila* is the only hypocrealean hyperepiphyllous parasite with an Afro-American distribution, just like its bi-continentally distributed host. In Costa Rica, it occurs sympatrically with *B. perianthiicola* in the same small area. *Bryocentria gynophila* and *B. perianthiicola* posses quite distinct, indented ascospores with a cyanophilous band. They differ by the number of perithecia formed per perianth, their size and position within the perianth, size of asci and ascospores, and host selection (see key, Tab. 1, and Döbbeler 1998).

Both species described in *Nectria* are transferred to *Bryocentria*, as they have few characters in common with *N. cinnabarina* (Tode) Fr., the type of the genus. The type species of *Bryocentria, B. brongniartii* (P. Crouan & H.Crouan) Döbbeler, is a biotrophic parasite of *Frullania dilatata* (Döbbeler 2004). Like several further species, including *B. phaeocarpa* (see below), it

obligately perforates the host leaves. *Bryocentria gynophila* behaves in the same way when it perforates the one cell layer thick perianth, a tubular sheath which is anatomically derived from modified fused leaves (Damsholt 2002). Features that both *Bryocentria* species share with most of their congenerics are the hyphal mat covering the excipulum, the numerously formed small asci, and the minute ascospores with a cyanophilous circular zone at the cross-wall.

4. *Bryocentria manubriata* Döbbeler, Karstenia 50: 15 (2010)

Type: Costa Rica, Prov. Alajuela: Southern surroundings of the volcano Arenal, Parque Nacional Arenal, ca. 600 m, 11 Mar 2008, P. Döbbeler 8652 (holotype USJ).

Perithecia on and between the leaves, subglobose or longer than wide, colourless to yellowish, without or with few short setae, 150-200 × 100-150 µm. Excipular cells (3-)5-11(-18) µm with cyanophilous walls; surface loosely covered by adjacent hyphae. Asci 24-40 × 5-7 µm, 8-spored, numerous. Ascospores rod-shaped with rounded ends, 1-septate, colourless, (8-)8.5-10(-11) × 2 µm, septum cyanophilous (Döbbeler 2010b, Fig. 2: a-g).

Host: Lejeuneaceae, sp. indet.

Known geographical distribution: Costa Rica.

5. *Bryocentria merospora* Döbbeler, Karstenia 50: 17 (2010)

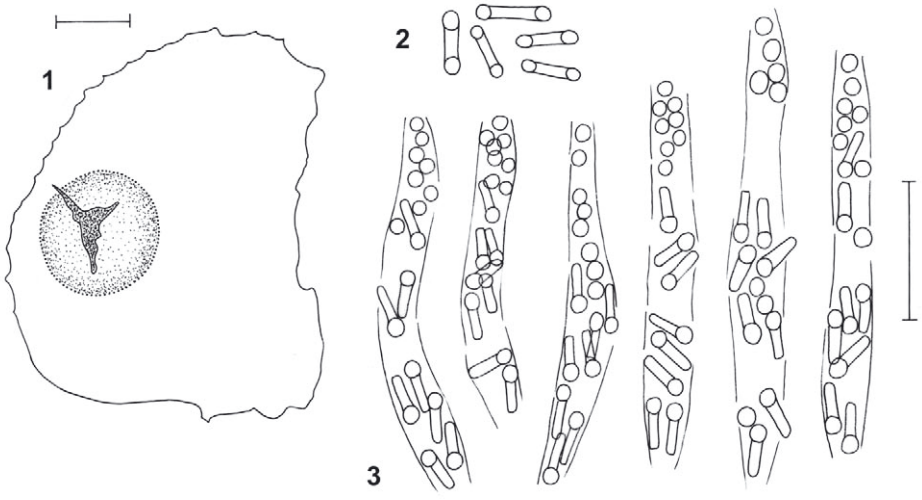

Fig. 3: *Bryocentria merospora* (P. Döbbeler 8905). 3.1 Perithecium perforating a host leaf, dorsal view, leaf tissue torn off. Scale bar = 100 µm. 3.2 Ascospores observed in developing asci, one of the globose cells not yet broken off. 3.3 Mature asci with dissolving walls and disarticulated spores; most of the globose part-spores concentrated in the upper ascus half. Figs 3.2, 3.3 scale bar = 10 µm.

Type: Costa Rica, Prov. Limón: Swamp forest near Tortuguero at the Carribean coast, 10 m, 21 Feb 2007, P. Döbbeler 8621 (holotype USJ).

Perithecia leaf-perforating, globose, golden-yellow to yellowish, without or with few short setae, 140–170 µm diam. Excipulum with rectangular to rounded, 5–10 µm large cells with cyanophilous walls; surface loosely covered by adjacent hyphae. Asci (16–)22–34(–38) × (3–)3.5–5(–5.5) µm, numerous, initially with 8 dumbbell-shaped, 3-celled ascospores, one of the end-cells soon breaking off resulting in 16 dimorphic part-spores still lying in the asci (8 pin-shaped and 2-celled, 8 globose and 1-celled). Ascospores: pin-shaped part-spores (3.5–)4–4.5(–5) µm long, rod-shaped cell ca. 1 µm wide, globose cell 1–1.5 µm wide, globose part-spores of the same size, the latter eventually concentrating in the apical ascus region (Döbbeler 2010b, Fig. 3: a–l).

Host: Lejeuneaceae, sp. indet.

Known geographical distribution: Costa Rica, French Guiana.

Additional specimen examined: French Guiana: Matoury, Roura, route to Kaw (D6), Sentiel Botanique, 04°30' N, 52°10' W, 100 m, 25 July 2009, L. Beenken (P. Döbbeler 8905 in M, only illustration).

6. *Bryocentria perianthiicola* (Döbbeler & J.Carranza) Döbbeler, comb. nov.

Basionym: *Nectria perianthiicola* Döbbeler & J.Carranza, Revista Biol. Trop. 41: 205 (1993).

MycoBank. MB 814654

Type: Costa Rica, Prov. Heredia: Finca La Selva cerca de Puerto Viejo, en los alrededores de la estación de la OET, 50 m, 31 Mai 1990, P. Döbbeler 6378 (holotype USJ).

Perithecia perianth-inhabiting, (sub)ovoid or pyriform, pale yellowish, apically brown, without setae, 140–260 × 120–210 µm. Excipulum 15–20 µm thick, outer layer composed of irregular hyphae 1.5-4 µm wide, with thick walls. Asci (38–)45–55(–58) × 4–5.5 µm, 8-spored. Ascospores subglobose to ellipsoidal, often depressed at one or both ends (even when turgid) and then almost cube-shaped, 1-septate, colourless, (4.5–)5–7(–8) × 4–5(–5.5) µm; epispore smooth; spores with a central cyanophilous band up to 1 µm wide. Hyphae mainly intercellular. Conidiomata superficial at the perianth base between the leaves, pulvinate, colourless, conidiogenous cells bottle-like; neck 5–8 µm long; conidia globose, colourless, 3.5–4.5 µm diam. (Döbbeler & Carranza 1993, Fig. 3: 1–5, Döbbeler 2010a).

Host: *Taxilejeunea* sp.

Known geographical distribution: Costa Rica.

Remarks: Perithecia arise singly within the upper part of the perianths, using the natural opening for spore dispersal. Conidiomata were not observed at the base of all perithecia-bearing perianths, but some are present in all known collections. *Bryocentria perianthiicola* has the same ascospore type as *B. gynophila* (see above). The conidiogenous cells are the first asexual state reported in *Bryocentria*.

7. *Bryocentria phaeocarpa* DÖBBELER, sp. nov.

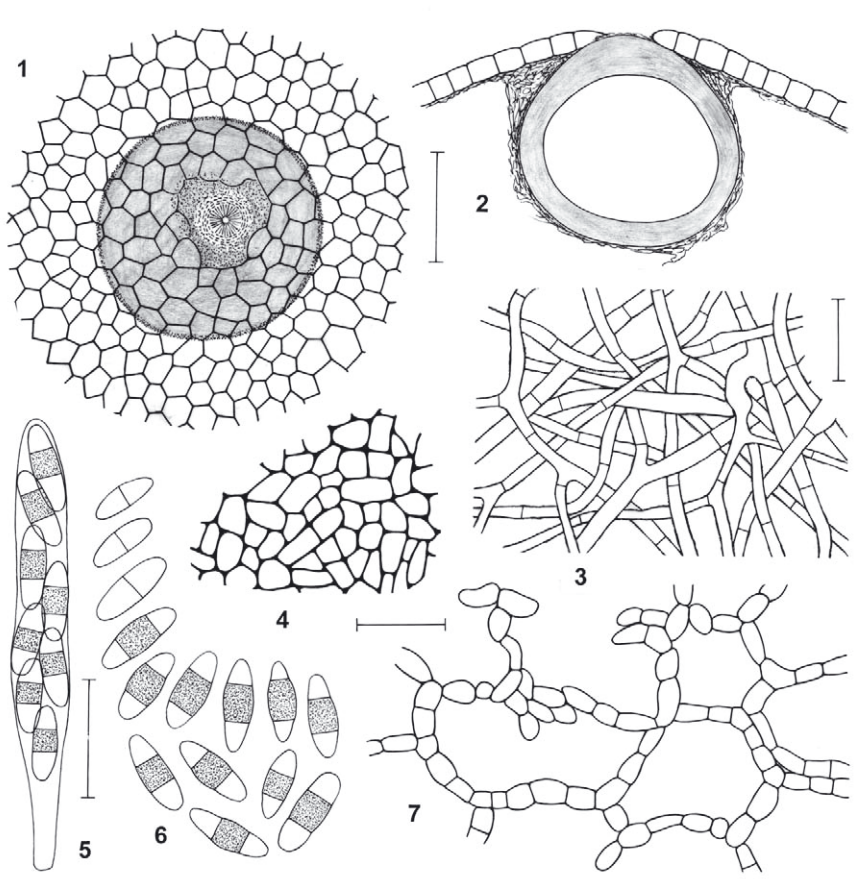

Fig. 4: *Bryocentria phaeocarpa* (holotype). 4.1 Perithecium perforating a host leaf, dorsal view, leaf cells at the perforation point replaced by excipular tissue. 4.2 Longitudinal, almost medium section through leaf-perforating perithecium. 4.3 Irregularly oriented hyphae covering the excipulum. 4.4 Excipular cells of a young perithecium seen from above. 4.5 Ascus. 4.6 Ascospores, cyanophilous band (stippled) obscuring the central septum; the upper three spores atypical. 4.7 Hyphae following the anticlinal host cell walls. Figs 4.1, 4.2 scale bar = 75 µm. Fig. 4.3 scale bar = 15 µm. Figs 4.4, 4.7 scale bar = 10 µm. Figs 4.5, 4.6 scale bar = 10 µm.

MycoBank: MB 814645

Etymology: *Phaeokarpos* (gr.) = with dark-coloured fruits; refers to the brown perithecia.

Type: Madagascar, Central East Madagascar: Degraded montane rainforest on Mt. Ambatokirijy at the South edge of Andasibe (Perinet), Forest Reserve, 950–1000 m, 18°57'15'' S, 48°26'0–20'' E, 3 Oct 1994, T. Pócs & A. Szabó 9488/AT (holotype EGR).

Perithecia leaf-perforating, globose, apically flattened, collapsed when dry, light to dark brown with a tint of red, without setae, surface tomentose, 100–160 µm diam. Ostiole inconspicuous, punctiform, ostiolar canal filled with radially oriented periphyses. Excipulum (as seen from above) with dark brown, irregularly oriented, more or less adjacent hyphae; hyphae 2–3(–4) µm wide with a rough or irregularly warty surface. Excipular cells sinuous, ca. 4–10 (–15) µm, with dark brown walls, excipular cells usually hidden by hyphae. In section, wall 15–20 µm thick laterally, surface uneven due to projecting hyphae. Below the outer hyphal layer of the excipulum there are several layers of rectangular, colourless, tangentially oriented, 4–10 µm long cells, the innermost cells are very thin-walled, narrow and very elongated; excipular cells cyanophilous. No colour change in KOH. Asci mostly cylindrical, thin-walled, without apical structures, sessile, numerous, (32–)36–42(–46) × (3.5)4–5(–6) µm, 8-spored, lining the lower and lateral excipulum, subhymenial tissue poorly developed. Ascospores narrowly ellipsoidal to fusiform, ends more or less rounded, colourless, 1-septate, septum rarely identifiable because it is covered by a cyanophilous, circular band, (5.5–)6.5–8.5(–9) × (2–)2.5–3(–3.5) µm; cyanophilous part often barrel-shaped and distinctly protruding, (2–)2.5–3.5(–4) µm wide; epispore outside the band pale blue in CB; ascospores 1- or 2-seriate within the asci. Hyphae variable, brown, ramified and anastomosing, superficially growing mainly over the ventral side of the host cells; hyphae close to the perithecia like those of the excipulum, further away they merge into short, barrel- to sausage-shaped, (1.5–)2–3.5 µm wide and 2–5 µm long cells that follow the anticlinal cell walls of the leaf; single hyphal cells sometimes wider than long; hyphae sometimes form several strands side by side and even form small pellicles; short subglobose hyphae also occasionally intracellular. Anamorph not observed.

Host: *Radula flaccida.*

Known geographical distribution: Madagascar, Tanzania.

Remarks: Perithecia usually develop singly on a host leaf, occasionally two or three have been observed on the same leaf. Leaves at the perforation point are not or slightly protruding. When seen from above, the exposed disc-like perithecium apex not covered by leaf cells measures about 50–65 µm in diameter. The outer part is brown and bordered by entire leaf cells. The inner colourless part with the central ostiole measures ca. 25–35 µm in diameter. The

species apparently behaves necrotrophically, but this should be corroborated using fresh material.

Bryocentria phaeocarpa is a well-defined species characterized by its persistent brown colour. The eight congeneric species (Döbbeler 2010b, Nordén et al. 2015) have orange-red to yellow perithecia. In the dry state, their pigments soon begin to disappear, eventually resulting in completely colourless ascomata.

The new species seems to be most closely related to *B. aequinoctiali*s (see above). The ascospores of both species are similar in shape and size, and both possess a well developed cyanophilous band. However, apart from the colour of the ascomata and hyphae, *B. aequinoctialis* has a distinctly cellular excipular structure (in surface view). There are further differences with regard to the preferred microniche, host selection and geographical distribution.

Additional specimen examined: Tanzania: Amani, 1911, K. Braun (M).

Bryonectria Döbbeler, Nova Hedwigia 66: 334 (1998)

Different *Bryonectria* species tend to grow intermingled on Lejeuneaceae occupying the same phorophyte leaf, and even on the same shoot or leaf of the host plant. A number of hitherto undescribed species have been observed. A reliable identification should be based on features of the ascomata and ascospores in combination with appressorium type. There may be a high degree of host specialization. This aspect would merit more attention in future studies.

The following characters distinguish all the *Bryonectria* species treated here from similar genera. If setae are present they are short, blunt and extremely thick-walled. The gelatinous excipulum is composed of irregularly ramified and anastomosing hyphal cells with thick, merging walls and very reduced lumina of varying width. The hymenial structures are usually recognisable through the excipulum using transmitted light. The excipular cells, as seen from the outside, hardly react with CB – apart from those in the uppermost part of the perithecia. The blue coloration of the periphyses within the ostiolar canal, which shine through the ascoma apex, is typical. In a few cases individual vividly coloured perithecia were found among hyaline ones. It is not clear whether they belong to species with typically colourless ascomata. In squash preparations asci emerge separately and float freely, or several asci connected by ascogenous hyphae may form small clusters. The hyphae grow superficially over both leaf sides and over the stem. They usually show a strong preference for the anticlinal host cell walls. The hyphal lumen is reduced and often less wide than the thickness of the surrounding wall. Intrahyphal hyphae are usually present. A curious, possibly more frequently occuring structure of unknown function was repeatedly observed on the appressoria. The appressorial cell (e.g. *B. clandestina*, Fig. 6.9) or one cell of more-celled

appressoria (e.g. *B. cyclopoda*, Fig. 7.6) produces a peg- or neck-like, minute outgrowth, which is reminiscent of the upper part of a conidiogenous cell. Anamorphs have been observed in four of the eight *Bryonectria* species. One species has compact conidiomata and three species form bottle-shaped conidiogenous cells. They may be irregularly spaced or located adjacent to each other on the hyphae. At least some of the phialides seem to be perpendicularly oriented to the substrate.

Besides the following eight species, *Bryonectria* includes ten non-phyllosphere dwelling species on liverworts and mosses of different ecology and systematic position. It has a well-defined relationship within the Bionectriaceae and, after *Epibryon* (Chaetothyriales), forms the second largest genus of perithecial bryophilous ascomycetes.

8. *Bryonectria calopoda* Döbbeler, sp. nov.

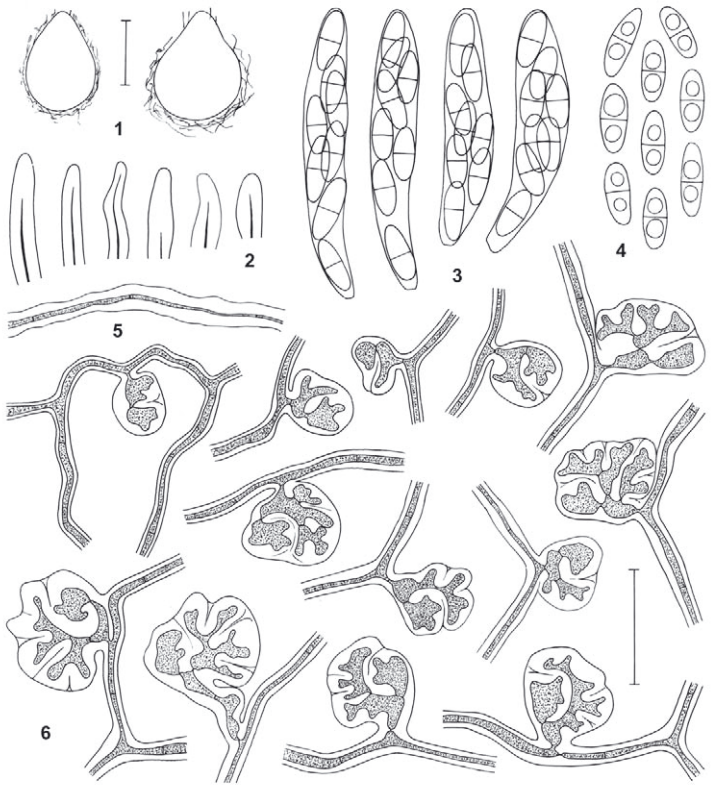

Fig. 5: *Bryonectria calopoda* (holotype). 5.1 Perithecia in outline. Scale bar = 75 µm. 5.2 Setae. 5.3 Asci. 5.4 Ascospores. 5.5 Extremely thick-walled hypha. 5.6 Three- and four-celled appressoria on hyphae, right a five-celled appressorium, above four immature appressoria. Figs 5.2–5.6 scale bar = 20 µm.

MycoBank: MB 814646

Etymology: *Kalos* (gr.) = beautiful, *pous* (gr.) = foot; refers to the attractive appressoria (hyphopodia).

Type: Costa Rica, Prov. Cartago: Orosi-Tal, Umgebung von Tapantí, Waldränder an der südlichen Flußseite kurz östlich der Brücke (Straße 224) über den Río Grande de Orosi, 1200 m, 26 May 1990, P. Döbbeler 6363 (holotype USJ, isotype M).

Perithecia on the ventral leaf margin, subpyriform, yellowish to ochre, whole surface uneven, tomentous, usually with some short setae at the apex, 95–140(–150) × 75–100 µm. Setae up to 15(–25) µm long. Excipulum composed of irregularly ramified and anastomosing thick-walled hyphae with strongly reduced lumina, lateral excipular wall in optical section 8–11 µm thick. Asci more or less cylindrical, straight or slightly bent, 40–51 × 8–10(–11) µm, (7-)8-spored. Ascospores narrowly ellipsoidal, sometimes slightly asymmetrical, 1-septate, not constricted at the septum, colourless, with one large guttule in each cell, (10–)11–13 × (3.5–)4–5 µm, irregularly biseriate in the asci; epispore delicately rough and slightly reacting with CB. Hyphae colourless, 2.5–4(–4.5) µm wide. Appressoria formed laterally on the hyphae, variable, sessile, almost circular with an undulating margin when seen from above, 15–20 µm in the largest diam., consisting of 3 or 4 strongly lobed cells with merging, up to 5(–7) µm thick walls, the basal cell of appressorium connected to the hypha not or hardly lobed. Anamorph not observed.

Host: Lejeuneaceae, sp. indet.

Known geographical distribution: Costa Rica, only type collection.

Remarks: Several perithecia may develop on heavily infected leaves. In such cases, the leaves are stuck together by a well-developed mycelium. The species behaves biotrophically.

Bryonectria calopoda seems to be most closely related to *B. lobopoda*, which differs by having slightly shorter, glabrous perithecia, shorter asci, smaller ascospores and smaller, less elaborate appressoria that consist of two or three cells instead of three or four as in *B. calopoda*. The latter infects a Lejeuneaceae whereas *B. lobopoda* occurs on *Radula flaccida*.

9. *Bryonectria clandestina* Döbbeler, sp. nov.

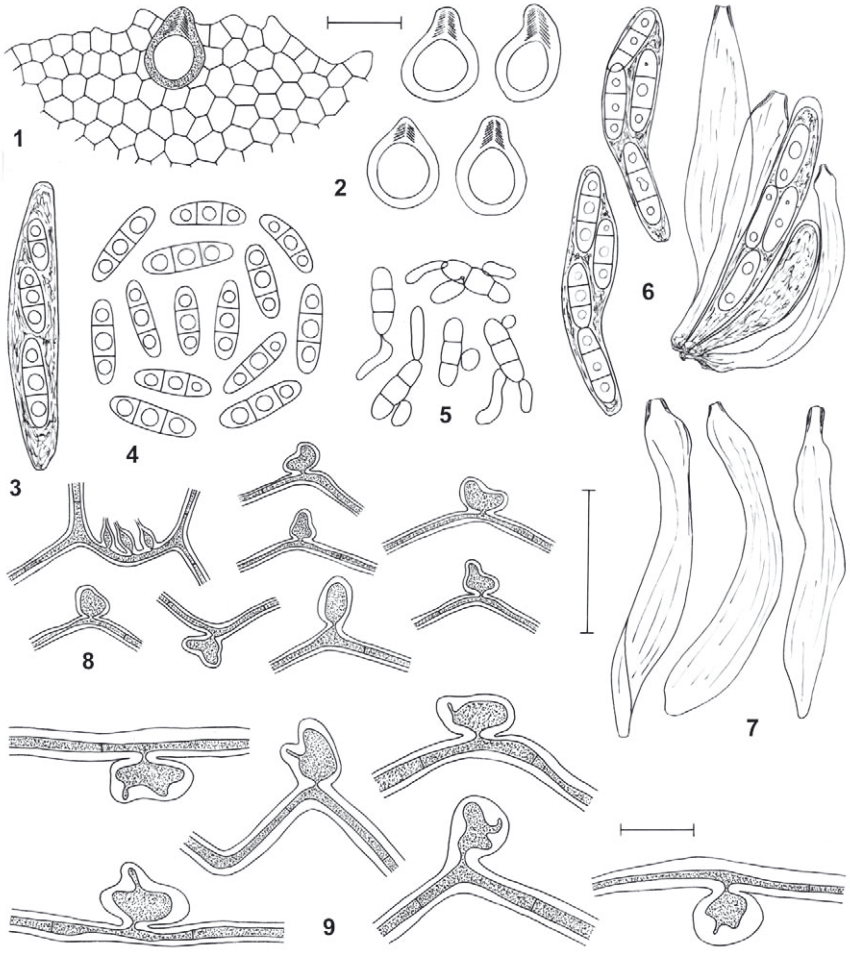

Fig. 6: *Bryonectria clandestina*. 6.1 Perithecium on the leaf border, ventral view. 6.2 Perithecia. 6.3 Atypical ascus with three spores, one of them two-celled and very small. 6.4 Ascospores. 6.5 Germinating ascospores (lying on a leaf surface). 6.6 Two mature asci and a group of immature and discharged asci. 6.7 Discharged, collapsed asci, showing the typical constricted apex. 6.8 Hyphal appendages: appressoria and three conidiogenous cells (above left). 6.9 Appressoria on hyphae, each with a peg-like outgrowth. Scale bar = 10 µm. Figs. 6.1, 6.2 scale bar = 100 µm. Figs. 6.3–6.8 scale bar = 20 µm. Figs. 6.1, 6.2 P. Döbbeler 6386. Figs. 6.3, 6.4, 6.6, 6.7 P. Döbbeler 8630. Fig. 6.8 P. Döbbeler 6740. Figs. 6.5, 6.9 Lücking.

MycoBank: MB 814647

Etymology: *Clandestinus* (lat.) = hidden, concealed; refers to the inconspicuous perithecia on the ventral leaf sides.

Type: Costa Rica, Prov. Limón: Parque Nacional Braulio Carrillo, Umgebung der Station der Guardaparques im untersten Teil des Parks, kurz östlich der Schnellstraße nach Guápiles,

Sendero "Quebrada Gonzales", 540–600 m, on undetermined Lejeuneaceae, 5 Mar 2008, P. Döbbeler 8660 (holotype USJ).

Perithecia on the ventral leaf margin, conical to pyriform, hyaline, without setae, 70–100(–130) × (55–)60–80(–90) µm. Ostiolar canal lined with upwards oriented periphyses. Excipulum composed of irregularly ramified and anastomosing, thick-walled hyphae with strongly reduced lumina, the lateral excipular wall in optical section 6–8 µm thick. Asci narrowly ellipsoidal to claviform, straight or sometimes bent, (25–)28–45(–50) × 6–9 µm, 4-spored, few mature asci per perithecium formed; empty asci extended (–55 µm) and laterally collapsed. Ascospores narrowly ellipsoidal to cylindrical with rounded ends, 2-septate, sometimes slightly constricted at the septa, colourless, (9–)10–13.5 (–14) × 3–4(–4.5) µm, with one large guttule per cell; discharged ascospores lying on the leaves germinating with an appressorium. Hyphae colourless, 2–4 µm wide. Appressoria laterally sitting on the hyphae, 1-celled, in surface view more or less elliptical with a sinuate outline, usually formed upon the cell corners, 4–7(–8.5) µm in the largest diam; longitudinal axis partly perpendicular to the hyphae of origin, partly horizontally oriented; appressoria sometimes with a delicate peg-like 1–1.5 µm long outgrowth of unknown function (often hard to observe); appressoria occasionally growing out resulting in an intercalary position. Conidiogenous cells phialidic, formed laterally on the hyphae, sessile, ca. 5–7 × 3 µm (only few times seen); conidia not observed.

Hosts: *Cyclolejeunea convexistipa* (Lehm. & Lindenb.) A.Evans, *C. peruviana* (Lehm. & Lindenb.) A.Evans, Lejeuneaceae, sp. indet.

Known geographical distribution: Costa Rica, Ecuador.

Remarks: *Bryonectria clandestina* is a rather frequent biotrophic hyperepiphyll in Costa Rica, but fruit-body density is usually low. The species is distinguished by having small perithecia and its ascus and ascospore features. The asci are four-spored from the earliest observable stages. A large perithecium contained 35 mature asci and a number of already empty ones. Both transverse spore septa are inserted at the same time. *Bryonectria cyclopoda* is very similar in habit to *B. clandestina* and may even occur on the same host plant. It deviates by having larger, two-celled ascospores and circular, three-celled appressoria. The formation of three-celled ascospores combined with four-spored asci is found in several species of *Bryonectria* and occurs in the following non-hyperepiphyllous species: *B. aphanes, B. biseptata, B. racomitrii* and *B. tricellularis.*

Additional specimens examined: Costa Rica, Prov. Alajuela: Karibische Seite der Cordillera de Tilarán, Reserva Forestal des San Ramón [= Reserva Biológica Alberto Manuel Brenes], Umgebung der Station am Río San Lorencito (nordwestlich San Ramón), um 850 m, on *C. convexistipa* and Lejeuneaceae, 9 Dec 1987, C. Bayer (P. Döbbeler 6386 in M); in the same region, 850–900 m, on Lejeuneaceae, 21 May 1988, P. Döbbeler 6321 (NY); in the same region, 850–950 m, on *C. convexistipa*, 24 Feb 1990, P. Döbbeler 6740 (USJ); in the same region, 850–950 m, on Lejeuneaceae,

1 Dec 1990, P. Döbbeler 7134 (M); in the same region, 850–950 m, on *C. peruviana*, 1 Mar 2007, P. Döbbeler 8627 (NY), on Lejeuneaceae, 1 Mar 2007, P. Döbbeler 8630 (NY). Südliche Umgebung des Vulkans Arenal, Parque Nacional Arenal, ca. 600 m, on Lejeuneaceae, 11 Mar 2008, P. Döbbeler 8641 (USJ). Prov. Limón: In the same region as the holotype collection, but ca. 540 m, on Lejeuneaceae, 21 Feb 2007, P. Döbbeler 8617 (M, only illustration). – Ecuador, Prov. Pichincha: "Guajalito" Biological Station, 45 km W of Quito on W slope of the Sierra Occidental (km 59 of old road to Sto. Domingo de los Colorados), 00°09' S, 78°39' W, 1800 m, on Lejeuneaceae, May 1996, R. Lücking (M).

10. *Bryonectria cyclopoda* Döbbeler, sp. nov.

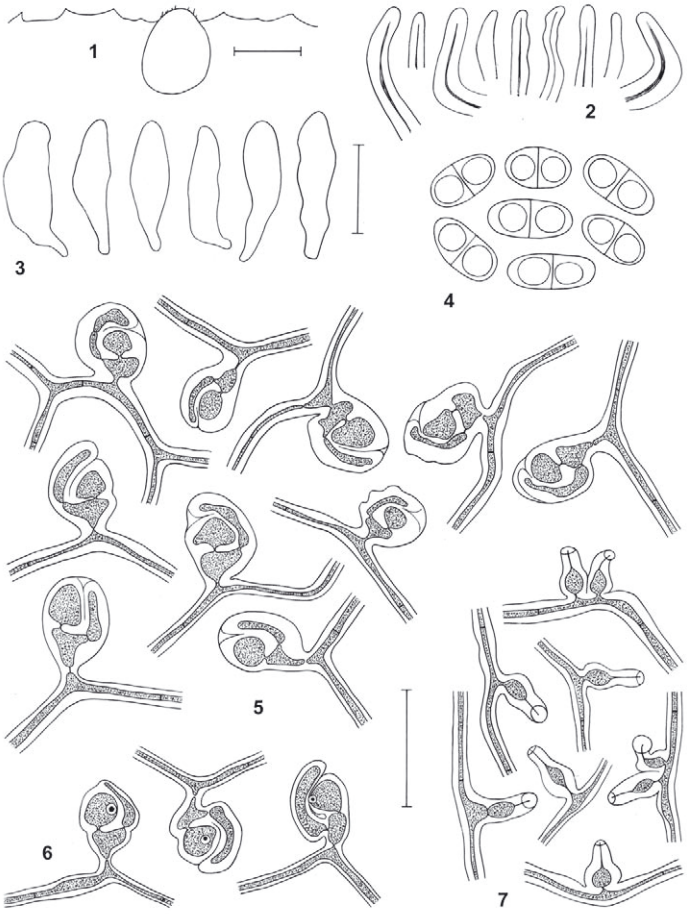

Fig. 7: *Bryonectria cyclopoda*. 7.1 Perithecium on the leaf border in outline, ventral view. Scale bar = 75 µm. 7.2 Setae. 7.3 Asci, all from one perithecium. Scale bar = 15 µm. 7.4 Ascospores. 7.5 Appressoria on hyphae, upper left show a four-celled appressorium. 7.6 Three appressoria, each with a peg-like outgrowth oriented perpendicularly to the appressorium surface. 7.7 Conidiogenous cells on the hyphae. Figs. 7.2, 7.4–7.7 scale bar = 20 µm. Figs. 7.1, 7.6 P. Döbbeler 8682. Figs. 7.2–7.5, 7.7 holotype.

MycoBank: MB 814648

Etymology: *Kyklo*s (gr.) = circle, *pous* (gr.) = foot; refers to the shape of the appressoria (hyphopodia).

Type: Costa Rica, Prov. Alajuela: Karibische Seite der Cordillera de Tilarán, Reserva Forestal de San Ramón [= Reserva Biológica Alberto Manuel Brenes], Umgebung der Station am Río San Lorencito (nordwestlich San Ramón), um 850 m, 9 Dec 1987, C. Bayer (holotype P. Döbbeler 6388 in USJ, isotype P. Döbbeler 6388 in M).

Perithecia on the ventral leaf margin, ovoid to subpyriform, hyaline, (100–)110–145 × (70–)80–110(–130) µm, surface apically sometimes uneven. Setae missing or, if present, notably in the upper part, up to 10(–15) µm long. Excipulum composed of irregularly ramified and anastomosing, thick-walled hyphae with strongly reduced lumina, lateral excipular wall 10–12 µm thick (in optical section). Asci irregular in outline due to spore position, sessile or with a short stalk, (40–)45–55(–60) × (10–)12–16(–18) µm, 8-spored. Ascospores ellipsoidal to ovoid, 1-septate, colourless, (10–)11–13.5(–16) × (4.5–)5.5–6.5 (–7.5) µm, with one large guttule per cell, irregularly biseriate in the asci; epispore smooth. Hyphae colourless, (2–)2.5–4(–5) µm wide. Appressoria sitting laterally on the hyphae, nearly circular in outline, 3-celled, (10–)13–16(–17) µm in the largest diam. Condiogenous cells phialidic, sessile, 7.5–12 µm long and ca. 4–6(–7) µm wide in the lower part, neck straight or bent, 2.5–3.5 µm wide, often several phialides side by side on a hypha; conidia not observed.

Host: *Cyclolejeunea peruviana*.

Known geographical distribution: Costa Rica.

Remarks: This new species is a biotrophic parasite. There may be up to several mature perithecia on a leaf. Four-spored asci with four degenerating spores were observed several times. The cells of the appressoria are always arranged in the same pattern. A basal cell arising from a hypha gives rise to two additional cells; a more or less (semi)circular apical cell and an elongated, narrow cell that is adjacent to the apical one and which is slightly to semicircularly bent. The lateral cell has sometimes a slightly undulate outer wall. The above-mentioned tiny outgrowth (see under general remarks about *Bryonectria*) can sometimes be clearly identified in apical cells. Seen from above, the protuberance is up to 4 µm wide and situated near the adjacent cell (Fig. 7, 6). An additional cross-wall was found a few times in the lateral cell, forming a four-celled appressorium. If the lateral cell grows out, the appressorium migrates to an intercalary position.

Additional specimens examined: Costa Rica, Prov. Alajuela: With the same label information as the holotype specimen but: Sendero, north of the river, 850–950 m, 1 Dec 1990, P. Döbbeler 7135 (M). Prov. Limón: Atlantikküste, Parque Nacional Tortuguero, 0–5 m, 6 Mar 2008, P. Döbbeler 8682 (M).

11. *Bryonectria diplopoda* Döbbeler, sp. nov.

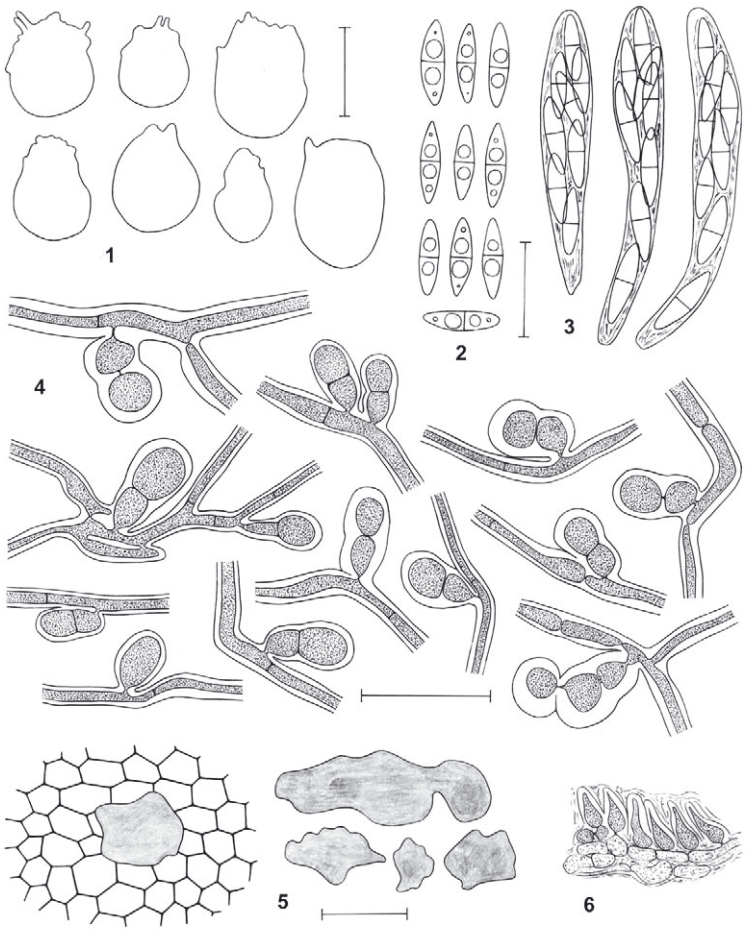

Fig. 8: *Bryonectria diplopoda* (holotype). 8.1 Perithecia in outline. Scale bar = 100 µm. 8.2 Ascospores. 8.3 Asci. 8.4 Appressoria on hyphae, bottom left a one-celled appressorium, right a three-celled one. 8.5 Variously shaped conidiomata, seen from above in outline. Scale bar = 40 µm. 8.6 Conidiogenous cells, lateral view. Figs. 8.2, 8.3 scale bar = 15 µm. Figs. 8.4, 8.6 scale bar = 15 µm.

MycoBank: MB 814649

Etymology: *Diplo-* (gr.) = double, *pous* (gr.) = foot; refers to the two-celled appressoria (hyphopodia).

Type: Colombia, Dep. del Quindío, municipio de Filandia: Vereda La Julia, carretera Filandia – La India, Finca La María, 1600 m, 3 Feb 1995, M. C. Vélez, D. Macías, M. L. Chacón & N. Rivero 4832 (holotype P. Döbbeler 6845a in M).

Perithecia on and between the leaves, colourless to hyaline, subglobose to almost ovoid, apically often irregular in outline due to the presence of setae

or protruding hyphae, (90–)105–150(–160) × (65–)80–120(–140) µm. Setae missing or, more often, present, individually or few of them forming clusters, very short or up to 25(–35) µm long and 4–6 µm wide at the base. Excipulum composed of irregularly ramified and anastomosing, thick-walled hyphae with strongly reduced lumina, lateral excipular wall in optical section 8–13(–15) µm thick. Asci mostly claviform, often slightly curved, with a short and broad foot, (40–)45–55(–58) × (8–)8.5–9.5(–10) µm, 8-spored. Ascospores fusiform to narrowly ellipsoidal, at most slightly asymmetrical, 1-septate, not constricted at the septum, colourless, with one large guttule in each cell, 12–13.5 × 3–4 µm; epispore smooth. Hyphae growing irregularly over the host cells, colourless, 2.5–4(–5) µm wide, sometimes completely covering parts of the host tissue. Appressoria formed laterally on the hyphae, with (1–)2(–3) cells, 9–14 (–16) × 5.5–8(–9) µm; cells are almost semicircular when seen from above and thick-walled, the distal cell is usually larger, not or somewhat constricted at the septum; appressoria usually not perpendicular to the hypha of origin but slightly or strongly inclined to it up to a position parallel to the hypha. Conidiomata cushion-shaped, forming thin patches of greatly varying shape and size, small patches tend to be circular, the larger ones elongated with an irregular outline, about 20–50(–100) µm in the greatest diam.; when seen from above the cells are angular or rounded, 2.5–4(–5) µm large, with thick and merging walls; in section consisting of two or few cell layers, outermost cells phialidic, ca. 5–8 µm long, neck with a delicate plasmatic strand inside; neck not visible in surface view; conidia not observed.

Host: Lejeuneaceae, sp. indet.

Known geographical distribution: Colombia, only type collection.

Remarks*:* Biologically, *Bryonectria diplopoda* behaves like a biotrophic parasite. It has two features not known elsewhere in the genus. The appressoria consist of two adnate, semicircular cells without undulating walls, and the phialides form a layer of cells that are connected laterally, and which are presumed to produce conidia. The compact angular texture of the isodiametric cells (in surface view) is typical for the conidiomata of this species. Conidiogenous cells are not rare within the genus, but they occur individually on the hyphae with one exception: *B. callicarpa* on *Frullania dilatata* has dome-shaped, up to 60 µm wide conidiomata. They leave a small hollow space between them and the host leaf surface. The phialides cover the inner side of the conidiomata and are oriented towards the host leaf (Döbbeler 1999). Perithecial initials in *B. diplopoda* can be found intermingled with conidiomata on the same leaf. The young ascomata differ from the conidiomata by not being flat but globose and by consisting of irregularly ramified hyphae.

12. *Bryonectria egens* (Corner) Döbbeler, comb. nov.

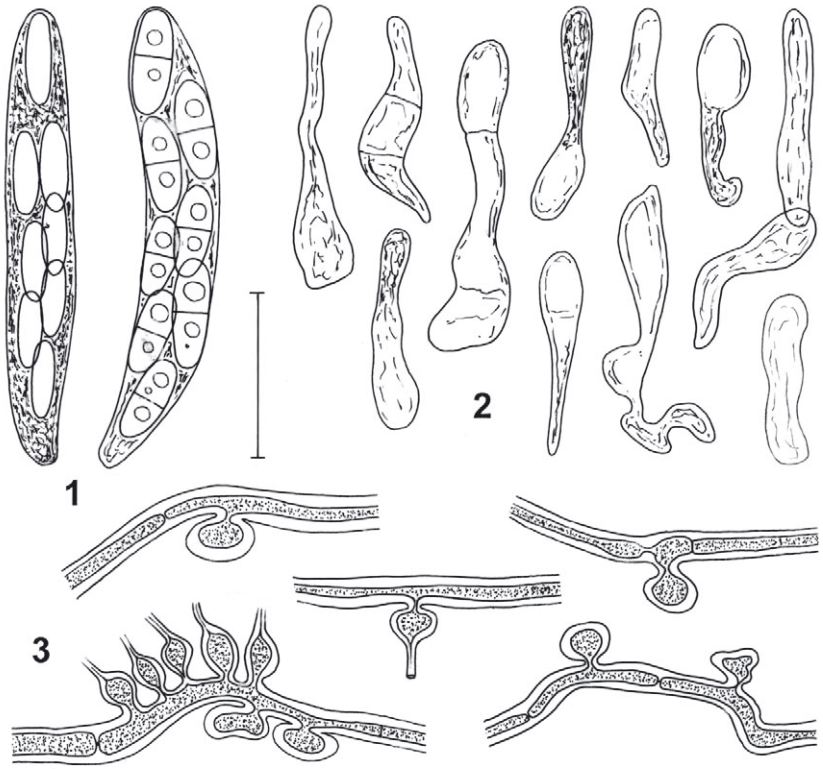

Fig. 9: *Bryonectria egens* (isotype). 9.1 Asci, the left one immature. 9.2 Apical paraphyses. 9.3 Appressoria and conidiogenous cells on hyphae. Figs 9.1–9.3 scale bar = 15 µm.

Basionym: *Nectria egens* Corner, Gard. Bull. Straits Settlem. 8: 135 (1935).

MycoBank: MB 814652

Type: Malaysia, Pahang: In silvis paludosis prope Tembeling, Nov–Dec 1930, E. J. H. Corner (isotype K).

Perithecia on the dorsal leaf sides, pyriform, red (when fresh; perithecia colourless in herbarium material), without setae, (75–)95–150 × (55–)65–105 µm, loosely attached. Ostiolar canal lined with periphyses oriented towards the ostiole; periphyses with orange-coloured granules. Excipulum composed of irregularly ramified and anastomosing, thick-walled hyphae with strongly reduced lumina (densely plectenchymatous), lateral excipular wall in optical section 8–20 µm thick, composed of 2 layers; outer layer 1–2 cells thick, of thick-walled, almost colourless hyphae, inner layer 2–3 cells thick, of thin-walled cells with orange-coloured granules. Apical paraphyses variable,

forming irregular filaments of 1 to few cells, with very delicate walls, ca. 19–29 × 5–9 µm. Asci cylindrical, narrowly ellipsoidal or enlarged in the middle or lower part, (33–)36–46(–51) × 7–10(–11) µm, 8-spored; empty, overmature asci up to 58 µm long. Ascospores ellipsoidal, often slightly asymmetrical, in the middle part not or slightly narrowed, 1-septate, 8–11 × 3.5–4 µm, with one hyaline or light yellow, 2–2.5 µm large guttule per cell; epispore delicately warted, cyanophilous. Hyphae colourless, (2–)2.5–4(–5) µm wide. Appressoria subcircular or elliptical in outline, sitting on the hyphae, 1-celled, 3–6.5 µm diam., predominantly formed above the cell corners. Condiogenous cells phialidic, sessile, up to 6(–7) µm long, often several sitting side by side on a hypha; conidia not observed (based on Corner 1935, Figs 1–3 and own observations of an isotype specimen (K)).

Host: *Leptolejeunea vitrea* (Nees) Schiffn. (syn. *L. corynophora* (Nees) Schiffn.).

Known geographical distribution: Malaysia (Pahang), only type locality.

Remarks: Studying an isotype revealed the presence of phialidic cells typical of the genus. The phialides and the similarly sessile appressoria are not easy to distinguish from each other due to their small size. Appressoria usually occur singly. They tend to be well spaced along a hypha and they are wider than long, whereas the phialides sometimes form short rows and are longer than wide.

Nectria egens, whose classification in *Nectria* was already questioned by Corner (1935), clearly belongs to *Bryonectria* Döbbeler, in spite of its red perithecia. Vividly coloured perithecia were also occasionally observed among other species treated here (see above). Most *Bryonectria* species have colourless or hyaline perithecia. However, *B. callicarpa* on corticolous *Frullania dilatata* has orange-red to yellow ascomata (Döbbeler 1999).

13. *Bryonectria lobopoda* Döbbeler, sp. nov.

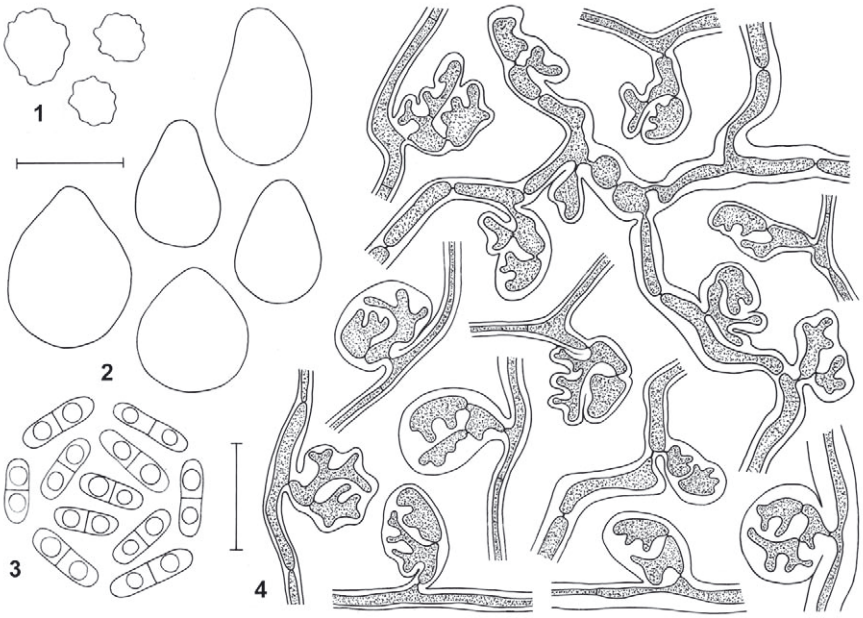

Fig. 10: *Bryonectria lobopoda* (holotype). 10.1 Primordia of perithecia, seen from above in outline. 10.2 Mature perithecia in outline. 10.3 Ascospores. 10.4 Appressoria on hyphae. Figs 10.1, 10.2 scale bar = 75 µm. Figs 10.3, 10.4 scale bar = 15 µm.

MycoBank: MB 814650

Etymology: *Lobos* (gr.) = lobe, leaf lobe, *pous* (gr.) = foot; refers to the shape of the appressoria (hyphopodia).

Type: Costa Rica, Prov. Cartago: Atlantic slope of the Cordillera de Talamanca, Jicotea village, about 55 km SE of Turrialba, small forest and plantations on finca (family Sasa) near the village, 09°49' N, 83°32' W, ca. 900 m, July 1997, A. Bernecker Lücking s. n. (holotype P. Döbbeler 9703 in M).

Perithecia on the ventral leaf margin, ovoid to subpyriform or conical with rounded apex and base, colourless, surface uneven, without setae, 80–120 × 60–110 µm. Excipulum composed of irregularly ramified and anastomosing, thick-walled hyphae with strongly reduced lumina, lateral excipular wall 8–11 µm thick (in optical section). Asci narrowly ellipsoidal, 33–42(–44) × 8–11.5 µm, 8-spored. Ascospores subcylindrical with rounded ends, 1-septate, often slightly asymmetrical, usually a little narrowed in the central region, not constricted at the septum, colourless, with one large guttule in each cell, (9–)10–12(–13) × 3–4 µm, irregularly lying in the asci; epispore smooth, not reacting with CB. Hyphae (2.5–)3–6(–7) µm wide, wall thickness variable and, in surface view, one side often thicker than the other. Appressoria are formed laterally on the hyphae, sessile, variable, almost circular or longer

than wide when seen from above, surface often irregularly undulate, 10–16 µm in the largest diam., thick-walled, consisting of 2 or more often 3 cells, both larger cells lobed, lobes usually oriented in the same direction, one or few lobes sometimes obviously oriented perpendicular to the substrate. Anamorph not observed.

Host: *Radula flaccida*.

Known geographical distribution: Costa Rica, only type collection.

Remarks:The biotrophic parasite *Bryonectria lobopoda* seems to be infrequent and many potential host specimens have been screened in vain. The type material is scanty, but heavily infected. Often several perithecia were observed in a curved line on the leaf margin. Ball-like aggregations of hyphae with merged cell walls arising from the mycelial network in this region are easy to recognize as ascoma primordials. They have a coarsely uneven surface. The ascospores are reminiscent of those of *B. egens*, but are somewhat larger.

14. *Bryonectria protonematis* Döbbeler, Nova Hedwigia 92: 370 (2011)

Type: Indonesia, Java: Bei Tjibodas, "bei 1400 M. c. fr. beobachtet", July 1898, Mar and Oct 1899, M. Fleischer (Fleischer, Musci Frond. Archip. Ind. Exs. 90, sub *E. tjibodensis*; holotype M, isotype H; an additional isotype reported here for NY).

Perithecia superficial on protonemal filaments, ovoid, subpyriform or conical with apical part often extended, without setae, (160–)180–340(–440) × (110–)120–180(–210) µm. Asci 62–80 × 7–13 µm, 8-spored. Ascospores ellipsoidal, 1-septate, colourless, (10–)11–14(–15) × (4–)4.5–5.5(–6) µm; epispore cyanophilous. Hyphae (2–)3–6(–8) µm wide, growing over the host filaments often forming a loose net or even a mantle around the filaments up to 15 (–20) µm thick. Appressoria sessile, in surface view elliptical, sometimes with sinuate margin, 1-celled, 6–11(–13) µm diam. (Döbbeler 2011b, Fig. 1: A–F, Fig. 2: A–D, Fig. 3: A–C).

Host: *Ephemeropsis tjibodensis* K.I.Goebel.

Known geographical distribution: Indonesia (Sumatra, Java, Celebes, Seram), Philippines (Mindanao), Papua New Guinea.

Remarks: Apart from few species of *Octospora* (Pezizales), *Bryonectria protonematis* is the only ascomycete reported so far to infect protonemata. Additionally, it is the only fungus known to parasitize an epiphyllous moss. *Ephemeropsis tjibodensis* is a widespread epiphyll in Southeast Asia. Its dense alga-like mats of protonemata are regarded as the most highly differentiated in mosses (Pressel & Duckett 2009). The moss itself belongs to the extremely reduced species. It mainly consists of persistent filaments that form sex organs (Frey & Stech 2009, Schofield 1985). *Ephemeropsis* retains its juvenile

features (neoteny), which is usually interpreted as an adaptation to ephemeral substrates (Gradstein 1997).

Additional specimens examined: Philippines: South Mindanao, Distr. Davao, July 1888, O. Warburg (NY). - Indonesia, Java: Tjibodas, ca. 1500 m, 15 Jan 1913, M. Fleischer (NY). - Indonesia, Celebes: Lore Kalimata National Park, 01°30' S, 120°16' E, 100 m, 24 Apr 1975. W. Meijer 9573 A (NY). – Indonesia, Maluku Islands, Seram: Seram Utara, Kecamatan, Gunung Roihelu, Sawai, Manusela National Park, 03°03' S, 129°14' E, ca. 1320 m, 26 Jan 1985, H. Akiyama 9843 (NY).

15. *Bryonectria* sp., Nova Hedwigia 66: 335 (1998)

Perithecia on the ventral leaf margin, ovoid to pyriform, without setae, hyaline, 80–125 × 55–80 µm. Asci 30–47 × 7–10 µm, 8-spored. Ascospores ellipsoidal, 1-septate, colourless, 8–11(–12) × 3–4 µm. Hyphae (2–)3–5(–6) µm thick. Appressoria elliptical in outline, often with sinuous margins, 1-celled, 6–10 µm diam. Anamorph not observed (Döbbeler 1998, Fig. 2: 1–6).

Host: *Radula flaccida*.

Known geographical distribution: Tanzania, only one collection.

The species is described and illustrated in detail by Döbbeler (l.c.) but not yet formally named because it can too easily be confused with the intermingled *Epibryon deceptor*. In addition, similar *Bryonectria*-species on Lejeuneaceae should be studied comparatively.

16. *Gynonectria intraspora* Döbbeler, Mycol. Prog. 11: 474 (2012)

Type: Costa Rica, Prov. Puntarenas: Cordillera de Tilarán, Monteverde Cloud Forest Reserve, ca. 1500 m, 10 Mar 2008, P. Döbbeler 8685 (holotype USJ).

Perithecia occur individually in the apical part of the perianths, globose to pyriform, light yellow, without setae, (190–)250–380(–410) × (170–)210–320(–350) µm. Excipulum composed of irregular hyphae with thick, merging walls and narrow lumina. Asci about 70–100(–118) × 8–17(–20) µm, when mature with 3–8 aggregated spores. Ascospores variable, dumbbell-shaped to almost cylindrical, with or without a single septum, colourless, (18–)25–50 (–84) µm long, (4–)5–9(–11) µm wide at the thickest and (2–)3–6 µm at the thinnest part; each ascospore with (1–)2(–3) internal spores (intraspores) lying freely in the plasma; intraspores fusiform to narrowly ellipsoidal, rod-shaped or dumbbell-shaped, (8–)10–20(–28) × (1.5–)2–5 µm. Hyphae growing superficially at the inner perianth wall and within the cell walls of gametophytic and sporophytic tissue in the perianth region. Conidiomata pulvinate, colourless, conidia globose, 3 µm diam. (Döbbeler 2012, Fig. 1: a–e, 2: a–d, 3: a–c, 4: a–h).

Host: *Odontolejeunea* sp.

Known geographical distribution: Costa Rica, Panama.

Remarks: The ascospores behave in a unique manner not known elsewhere among the ascomycetes. They produce a second spore generation endogenously, the intraspores. The intraspores lie freely within the cytoplasm of the mother spore, the primary ascospores. There are no continuous wall layers between both spore generations (Döbbeler 2012).

17. ***Nectria brenesii*** Döbbeler & J.Carranza, Revista Biol. Trop. 41: 203 (1993)

Type: Costa Rica, Prov. Alajuela: Cordillera de Tilarán, Reserva Forestal de San Ramón, 850–900 m, 21 May 1988, P. Döbbeler 6472 (holotype USJ).

Perithecia between the leaves, subglobose to pyriform, almost colourless, 150–190 × 130–180 µm. Setae usually present in the upper part of the perithecia, 5–30 × 2.5–5 µm. Excipulum gelatinous, with thick-walled cells arranged in an irregular, star-like form. Asci 26–36 × 4–6 µm, 8-spored at first, walls dissolving. Ascospores bacilliform, colourless, when immature bicellular, at maturity disarticulating at the septum, partial ascospores 1-celled, (5–)5.5–8 (–9) × (1.5–)2–2.5 µm. Hyphae 2–3 µm wide, with unequally thickened walls, growing irregularly over the host cells (Döbbeler & Carranza 1993, Fig. 1: 1–5).

Host: Lejeuneaceae, sp. indet.

Known geographical distribution: Costa Rica, only type collection.

Remarks: The older plant parts are the preferred sites of fruit-body formation. However, infection does not cause a visible effect on the host. *Nectria brenesii* and *Bryocentria merospora* are, so far, the only hyperepiphyllous species with disarticulating ascospores, a feature well-known in other Hypocreales (Rossman et al. 1999).

18. ***Nectria contraria*** Döbbeler, Nova Hedwigia 66: 354 (1998)

Type: Costa Rica, Prov. Cartago: CATIE bei Turrialba, sendero Espaveles zum Río Reventazón, 500–600 m, 24 Nov 1988, P. Döbbeler 6364 (holotype M, isotype CR).

Perithecia on or between the leaves, broadly ovoid to subpyriform, colourless, 100–150 × 80–110 µm, apically with some short (up to 25 µm long) setae, with thick, cyanophilous walls. Excipulum loosely covered by irregularly oriented hyphae. Asci 19–24(–27) × 4–6 µm, 8-spored. Ascospores colourless, 1-septate, one cell hemispherical, the other wedge-shaped, (5.5–)6–7 × 2.5–3.5 µm, the hemispherical cell partly oriented to the ascus tip, partly in the opposite direction. Hyphae 1.5–4 µm wide, superficial. Appressoria in surface view elliptical, in lateral, terminal or intercalary position, mostly 1-celled, ca. 5–11 × 4–6 µm. Haustoria intracellular, connected to the appressoria by a delicate perforation hypha (Döbbeler 1998, Fig. 13: 1–6, Fig. 14).

Host: *Radula flaccida*.

Known geographical distribution: Costa Rica, only type collection.

Remarks: The species is characterized by its ascospore features and an infection structure that closely resembles that of *N. hyperepiphylla* (see below).

19. ***Nectria hyperepiphylla*** Döbbeler, Sydowia 57: 183 (2005)

Type: New Caledonia, Grande-Terre, Prov. Sud: Monts Koghis-Dumbéa, ca. 15 km NNE from Nouméa, 22°14' S, 166°30' E, 550 m, 23 Aug 1994, K. & A. Kalb (holotype M).

Perithecia on the ventral leaf margin, ovoid to pyriform, colourless, 130–180 × 100–140 µm, apically with blunt, bristle-like hyphae up to 40(–60) µm long; surface covered by interwoven hyphae sometimes forming a dense, apically up to 30 µm thick layer. Excipulum with epidermis-like, 10–18 µm large cells. Asci 22–40 × 4 µm, dissolving, (3–)4-spored. Ascospores subcylindrical to narrowly ellipsoidal, 1-septate, colourless, (5.5–)6–7(–8) × 2–2.5(–3) µm; epispore finely rough, not reacting with CB. Hyphae finely rough, 1.5–2.5 (–3) µm wide, irregularly growing over the host cells. Appressoria elliptical in outline, lateral and sessile or terminal, 1- or 2-celled, thick-walled, (6–)9–12(–14) µm diam., forming intracellular haustoria (Döbbeler 2005, Figs 9–14).

Host: Lejeuneaceae, sp. indet.

Known geographical distribution: New Caledonia, only type collection.

20. ***Nectria lankesteri*** Döbbeler & J.Carranza, Revista Biol. Trop. 41: 204 (1993)

Type: Costa Rica, Prov. Cartago: Jardín Botánico Carlos H. Lankester de la Universidad de Costa Rica, al sureste de Cartago, 1360 m, 11 Nov. 1989, P. Döbbeler 6366 (holotype USJ).

Perithecia between the leaves, ovoid, orange, 130–180 × 100–150 µm. Setae straight or curved, very short or up to 35(–50) × 3–6 µm. Excipulum with isodiametric or irregular, 5–15(–20) µm large cells, often loosely covered by adjacent hyphae. Asci 20–31(–36) × 5–7.5(–8.5) µm, (6-, 7-)8-spored. Ascospores ellipsoidal, 1-septate, colourless, with thick walls and subglobose lumina, 5–6.5 × 3.5–4.5(–5) µm; epispore smooth or rough, slightly cyanophilous. Hyphae 1.5–3 µm wide, irregularly growing over the host cells (Döbbeler & Carranza 1993, Fig. 2: 1–3).

Host: Lejeuneaceae, sp. indet.

Known geographical distribution: Costa Rica, only type collection.

21. ***Nectria turrialbae*** Döbbeler & J.Carranza, Revista Biol. Trop. 41: 207 (1993)

Type: Costa Rica, Prov. Cartago: Monumento Nacional Guayabo, al Norte de Turrialba, 1100 m, 30 Dec 1989, P. Döbbeler 6346 (holotype USJ).

Ascomata on and between the leaves, subovoid, yellowish, 100–150 × 90–120 µm. Setae straight or curved, 5–25(–35) × 2.5–4 µm. Outer layer of excipulum with irregular hyphae. Asci 22–28 × 4–6 µm, (6–, 7–)8-spored. Ascospores ellipsoidal to subfusiform, 1-septate, colourless, thick-walled, (4–)4.5–5.5(–6) × 2.5–3.5 µm; epispore rough, slightly cyanophilous. Hyphae superficial on the host cells, (1.5–)2–3(–4) µm wide, with intracellular haustoria connected directly to a normal hyphal cell or to a lateral, appressorium-like hyphal projection (Döbbeler & Carranza 1993, Fig. 4: 1–6).

Host: Lejeuneaceae, sp. indet.

Known geographical distribution: Costa Rica, only type collection.

22. ***Ticonectria capta*** Döbbeler, sp. nov.

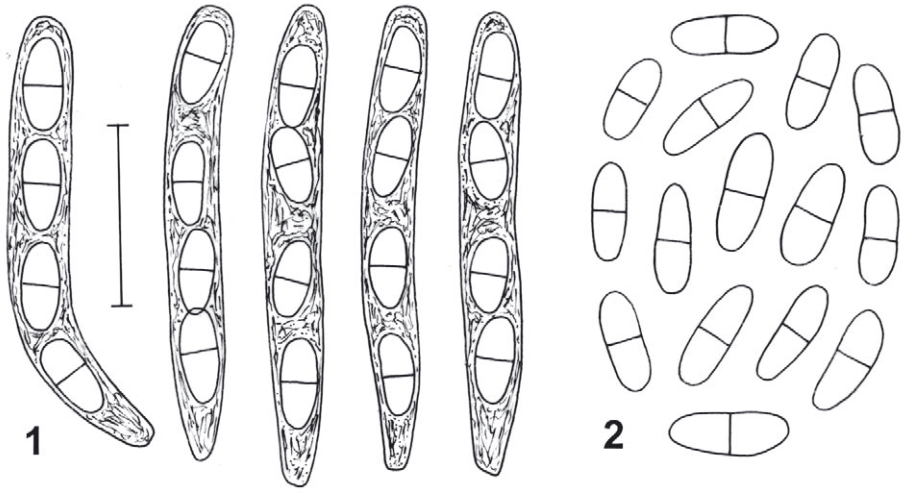

Fig. 11: *Ticonectria capta*. 11.1 Asci (Nyman, NY 02342264). 11.2 Ascospores (Fleischer, Exs. 509, B). Figs 1, 2 scale bar = 15 µm.

MycoBank: MB 814651

Etymology: *Captus*, participle of *capere* (lat.) = catch; the fungus is enclosed by the perianth.

Type: Indonesia, Java: Tjibodas, an feuchten Orten und Bachufern auf Phanerogamen und Filicesblättern, 1400–2000 m, July 1898, M. Fleischer (Fleischer, Musci Frond. Archip. Ind. Exs. 37, sub *Ephemeropsis tjibodensis*; host species intermingled), (holotype NY, isotype H).

All characters so far analyzed (hyphae not studied, anamorph not observed) agree well with the related *T. perianthii*. Both species can cause severe gall-like swellings and dark malformations of infected perianths. Asci and ascospores of *T. capta* have the following features: Asci 35–42 × 4.5–6.5 µm, 4-spored. Ascospores narrowly ellipsoidal, one cell usually a little wider than the other, spore diam. at the septum sometimes slightly less than in the midst of the broader cell, (7–)7.5–10(–11.5) × 3–3.5(–4) µm; epispore reaction with CB not clearly seen. Apart from ascospore shape, somewhat smaller size and number per ascus, the new species differs from *T. perianthii* by its host selection and geographical distribution.

Host: *Radula* sp. (sect. *Epiphyllae*).

Known geographical distribution: Indonesia (Java).

Remarks: The species was found independently, several times on *Radula* sp. in collections of *Ephemeropsis tjibodensis*. The liverwort grew intermingled with the moss on the same phorophyte leaves. All records (three belong to the same number of an exsiccate) consist of just a few perianths bearing perithecia. Nevertheless, the species is described as new for the following reasons: It has, like *T. perianthii*, rather conspicuous fruit-bodies and does not appear to be rare. *Ticonectria capta* is almost certainly present on duplicates of the indicated exsiccates as well as on Asian epiphyllous *Radula* populations bearing perianths.

Additional specimens examined: Indonesia, Java: Tjibodas, July 1898, E. Nyman (Plantae Javanicae 432bis, sub *Ephemeropsis tjibodensis*; host species intermingled; NY 02342264 and 02342274). Gedeh above Tjibodas, 1500 m, Feb 1913, M. Fleischer (Fleischer, Musci Frond. Archip. Ind. Polynes. Exs. 509, sub *E. tjibodensis*; host species intermingled; B, H, M).

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

Type: Costa Rica, Prov. Cartago: "CATIE bei Turrialba, sendero Espaveles zum Río Reventazón", 500-600 m, 24 Nov 1988, P. Döbbeler 6327 (holotype M, isotype CR).

Perithecia perianth-inhabiting, pyriform, nearly colourless to dark grey brown to almost black, without setae, 150–250 × 130–220 µm. Excipulum composed of thick-walled, irregularly arranged hyphae with merging walls and reduced lumina. Asci 45–60 × 6–8(–10) µm, 8-spored. Ascospores ellipsoidal to ovoid, 1-septate, colourless, 7–9(–10.5) × 4–5(–6) µm; epispore delicately rough, cyanophilous. Hyphae superficial on the inner perianth wall and within the cell walls of the junction tissue of gametophyte and sporophyte. Conidiomata between the leaves at the perianth base, pulvinate, colourless, conidiogenous cells slender; conidia globose, 1-celled, thick-walled, 6–8 µm diam. (Döbbeler 1998, Fig. 18: 1–5, Fig. 19: 1, 2, Fig. 20: 1–3; Döbbeler 2010a; Döbbeler & Hertel 2013, Fig. 22, distribution map).

Host: *Radula flaccida*.

Known geographical distribution: Honduras, Costa Rica, Surinam, French Guiana.

Remarks: Perithecia may develop alone or form clusters of up to ten located in the middle and lower part of the perianth. They perforate the perianth wall with their apices. Infected perianths vary greatly in appearance from unaltered to strongly deformed with dark, gall-like swellings and distortions at the site of perithecium formation. Early and/or heavy infection apparently inhibits the development of the perianths resulting in stunted, deformed shoots occupied by perithecia and conidiomata.

24. *Ticonectria testudinea* Döbbeler, Mycologia 102: 409 (2010)

Type: Costa Rica, Prov. Puntarenas: Cordillera de Tilarán, Monteverde Cloud Forest Reserve, ca. 1500 m, 10 Mar 2008, P. Döbbeler 8690 (holotype USJ, isotype M).

Perithecia perianth-inhabiting, pyriform, light or ochre-brown, apically darker, without setae, (210–)240–280(–310) × 170–240 µm. Excipulum composed of hyphae with merging walls and small lumina. Asci 50–75(–82) × 10–13(–14) µm, with 8 or fewer spores. Ascospores more or less ellipsoidal, colourless, (10–)11–14(–17) × (4.5–)5–7(–7.5) µm, with 2 dissimilar cells, the larger cell ellipsoidal with a truncated end and a thick, cyanophilous wall, the smaller one attached to the truncated end, semiglobose, thin-walled, 2–3 (–4) µm diam. Hyphae superficial on the inner perianth surface and between the cells and within their walls of the young sporophyte and the gametophytic stem (Döbbeler 2010a, Figs 13–21).

Host: *Cyclolejeunea convexistipa.*

Known geographical distribution: Costa Rica.

Remarks: The perithecia develop singly within the apical parts of the perianths. Analysis of hyphal distribution by longitudinal sections through infected perianths result in complex patterns. Hyphae concentrate in the gametophyte-sporophyte junction between and below the nutrient-rich transfer cells. The extremely delicate hyphal ramifications seem to indicate a haustorial function.

The oldest report of a bryophyte on living leaves was probably by Swartz in 1788, who described the hepatic *Jungermannia flava* Sw. (syn. *Lejeunea flava* (Sw.) Nees) from Jamaica (cited after Gradstein 1997). Almost 150 years later, Corner (1935) discovered the conspicuously red-coloured *Bryonectria egens* in Malaysia, the first hyperepiphyllous ascomycete to be recorded. And only now, we begin to realize that fungal parasites of epiphyllous liverworts are frequent and highly adapted members of the phyllosphere. They contribute to fungal diversity in tropical regions, add new morphological and ecological features to the ascomycetes, and enrich the knowledge of inter-kingdom

associations. The evolutionary explosion of the Lejeuneaceae is as extensive and intricate as that of their phorophytes, the angiosperms (Schuster 1979). This concept should be expanded to include fungal, especially hypocrealean, parasites that utilize epiphylls. Theodor Herzog stated in his "Geographie der Moose" (1926: 207) that "the most extraordinary and astonishingly inventive morphological and biological forms are hidden amongst the epiphylls" (translated from German). By adding a prefix of two syllables the same words characterize the fascinating novel group of phyllosphere fungi: The most extraordinary and astonishingly inventive morphological and biological forms are hidden amongst the hyperepiphylls.

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