

New species and records of *Bryocentria* – a hypocrealean genus of bryophilous ascomycetes

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The bryophilous genus *Bryocentria* (Hypocreales, Ascomycetes), with three known species, is augmented by four new taxa. These are *B. aequinoctialis*, *B. manubriata* and *B. merospora* on epiphyllous Lejeuneaceae (Hepaticae) from Costa Rica, and *B. septinensis* on *Sanionia uncinata* (Musci) from Finland. Some new records of *B. brongniartii* and *B. metzgeriae* are also presented. Characters important at the generic level are the possession of small, lightly coloured, almost glabrous perithecia, a cellular cyanophilous excipulum often loosely covered by adjacent hyphae, numerous, eight-spored asci with delicate walls, tiny, two-celled ascospores of differing shapes with a cyanophilous septum or band-like structure in most species, and an obligate occurrence on bryophytes. All species, apart from the biotrophic *B. brongniartii*, are necrotrophic parasites that cause discoloured islet-like infections. Several species perforate the leaves of hepatics with their developing perithecia. Host species belong to different systematic and ecological groups of bryophytes, predominantly hepatics. *Bryocentria merospora* features a novel type of ascospore. After disarticulating, the globose partial spores concentrate in the ascus apex. The three hyperepiphyllous *Bryocentria* species demonstrate the wealth of necrotrophic fungi in the phyllosphere of tropical rain forests.

Key words: hepaticolous, hyperepiphyllous, necrotrophic parasitism, Hypocreales, taxonomy.

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Introduction

The manifold associations between ascomycetes and bryophytes range from occasional occurrence to a strong specificity to certain host species where distinct microniches may be occupied. Genera such as *Dactylospora*, *Hymenoscyphus*, or *Muellerella* contain mainly non-bryophilous species but some are known to infect bryophytes. *Epibryon*, the largest genus of bryophilous ascomycetes with about 45 species, has four non-bryophilous members that grow

on lichens (Matzer 1996, Sérusiaux et al. 1999, Hoffmann & Hafellner 2000). In contrast, some genera are entirely obligately bryophilous, occurring only on mosses or hepatics. Examples include *Bryodiscus*, *Bryonectria*, or *Hypobryon*. In these cases speciation apparently took place after adopting the bryophilous way of life. The hypocrealean *Bryocentria* is another genus that invariably occurs on bryophytes. It is augmented here by the inclusion of four novel species.

Material and methods

Standard methods were used to describe the fungi. All measurements (apart from ascoma size) and illustrations were performed after staining with heated lactophenol-cotton blue (Merck 13741). Without phase contrast optics and staining, delicate structures like apical paraphyses or spore characters remain almost invisible. Extreme values of measured structures are given in brackets. Possible KOH colour changes of the perithecia and iodine reactions (Lugol's solution) were checked and found always to be negative. It was noted that vividly coloured perithecia may become completely colourless in the herbarium some years after collecting. Illustrations are presented to allow unambiguous identification of the newly described species. Huhtinen's statement (1994), that one learns more from a set of detailed camera lucida drawings than from a published paper, is especially true for these tiny and hidden fungi.

Bryocentria Döbbeler, Mycol. Progr. 3: 247. 2004 (Bionectriaceae, Hypocreales)

Perithecia formed on or between the host leaves or on their ventral side and perforating them, globose, ovoid or pyriform, soft-textured, 110–280 µm diam, when fresh, orange-coloured to yellowish, no colour change in KOH, herbarium material fading and finally completely colourless, surface more or less densely covered by 1.5–3(–5) µm wide, colourless hyphae with cyanophilous walls. *Setae* missing or few short setae surrounding the ostiolar region, setae apically rounded and thin-walled, up to 20 µm long and 2.5–5 µm wide at the base. *Ostiole* inconspicuous, punctiform, ca 5 µm diam; ostiolar canal lined with periphyses that can contain coloured droplets (fresh material). *Excipulum* coloured, in surface view with rectangular or slightly rounded cells (*textura angularis*), in middle and lower

part cells up to 15 µm wide, with cyanophilous, often somewhat irregularly thickened walls with pits, cells apically smaller, with elliptical to roundish lumina; excipulum in cross-section 10–17 µm thick, composed of several layers of flattened cells containing coloured droplets; innermost cells thin-walled and tangentially elongated. *Apical paraphyses* extremely delicate, forming irregular, sparsely branched chains of thin-walled, ellipsoidal to subglobose cells of greatly varying size, individual cells up to 20 (–30) µm long, 10 µm wide, orange droplets may be present; apical paraphyses filling dome-like space above hymenium and fixed at top of centrum, also between asci and connected to hymenial base, in squash mounts easily separated and friable. *Asci* unitunicate, in most cases cylindrical to slightly clavate, 20–60 × 3.5–7 µm, thin-walled and sometimes only spore packets visible at maturity, apically rounded, without visible apical structures, eight-spored, numerous; iodine reaction (Lugol's solution) negative. *Ascospores* ellipsoidal, fusiform or dumbbell-shaped, two-celled (but septum often hidden by cyanophilous band), colourless, 4.5–10 × 1–3.5 µm, often with a central cyanophilous band, uniseriate or irregularly biseriate within asci; central band most clearly seen in lactophenol-cotton blue using phase-contrast optics. *Hyphae* colourless, up to 3 µm wide, ramified with anastomoses, sometimes forming an arachnoid aerial mycelium at base of ascomata and between and upon leaves; hyphae also superficially growing over host cells. *Anamorph* not observed. Typically grows necrotrophically on ecologically and systematically diverse bryophytes.

Generic type: *B. brongniartii* (P. Crouan & H. Crouan) Döbbeler.

Key to the species of *Bryocentria*

1. Perithecia leaf-perforating, globose to subglobose, orange-coloured, 140–220 µm diam; ascospores 6.5–7.5 × 2–2.5 µm, dumbbell-shaped; biotrophic on *Frullania dilatata*; Europe *B. brongniartii*
– Not with this character combination; necrotrophic 2
2. Perithecia leaf-perforating, globose to subglobose, orange-coloured, 170–230 µm diam; ascospores 5.5–7.5 × 1.5–2 µm, fusiform; on *Radula complanata* and other corticolous hepatics; Europe *B. metzgeriae*
– Not with this character combination; on mosses in Europe or on epiphyllous hepatics in the tropics 3
3. On mosses; Europe 4
– On epiphyllous hepatics; in the tropics 5
4. Perithecia 200–280 × 140–220 µm; ascospores almost cylindrical to narrowly ellipsoidal, 5.5–7.5 × 1.5–2 µm; episporium smooth *B. cyanodesma*
– Perithecia 120–170 × 90–150 µm; ascospores doliiiform, 6–7 × 3–3.5 µm; episporium with delicate cyanophilous warts *B. septinensis*
5. Perithecia leaf-perforating; ascospores mostly pin-shaped consisting of a rod-like cell and a globose cell, up to 4.5 µm long and up to 1.5 µm wide *B. merospora*
– Perithecia superficially on or between the leaves; ascospores not pin-shaped 6
6. Ascospores almost rod-shaped with rounded ends, 8.5–10 × 2 µm, without a cyanophilous band *B. manubriata*
– Ascospores fusiform to ellipsoidal, widest at the middle part, 4.5–6 × 2.5 µm, with a strongly developed cyanophilous central band *B. aequinoctialis*

The species

Bryocentria aequinoctialis Döbbeler sp. nov.

– Fig. 1

MycoBank no.: MB518387

Etymology: *Aequinoctialis* (lat.) = equinoctial, relating to an equinox (equal lengths of night and day); due to occurrence in the tropics.

Perithecia superficialiter inter folia hospitis evoluta, subglobosa vel ovoidea, aurantiaca usque ad flava, 110–150 µm in diam, glabra vel nonnullis setis brevibus ornata. Excipulum cellulis rectangularibus, 3–8(–10) µm latis compositum, parietes cellularum cyanophili. Excipulum hyphis incoloratis plus minusve densis obtectum; KOH

ope non reagens. Asci unitunicati, cylindrici, 20–28 × 4–5 µm, octo-sporei; reactio jodi negativa. Ascosporeae fusiformes vel ellipsoidales, incoloratae, bicellulatae, 4.5–6 × 2.5 µm, pars centralis cingulo cyanophilo praedita. Hyphae non examinatae. Conidiomata non visa. Habitat parasitice in hepaticis epiphyllis familiae Lejeuneaceae laesiones decoloratas in hospite efficiens.

Typus: Costa Rica. Prov. Alajuela: Surroundings of the volcano Arenal, east of the Laguna de Arenal, ca 500 m alt., 2.III.2007 Döbbeler 8640 (USJ – Holotypus).

Ascomata superficially formed on infected plants, almost globose to ovoid, orange-coloured

to yellowish, (80–)110–150(–170) μm diam at the widest point, without setae or with few short setae apically near the ostiole. *Excipulum* in surface view with rectangular cells measuring 3–8(–10) μm , cell walls cyanophilous, sometimes pitted and thickened at the junctions; surface loosely covered by adjacent hyphae; no colour change in KOH. *Apical paraphyses* not observed. *Asci* unitunicate, cylindrical, (17–)20–30(–34) \times 4–5 μm , eight-spored; ascus wall delicate and disappearing early; iodine reaction (Lugol's solution) negative. *Ascospores* fusiform to ellipsoidal, often slightly asymmetric with one end more rounded than the other, colourless, two-celled, (4–)4.5–6(–6.5) \times (2–)2.5(–3) μm , uniseriate, cyanophilous central band strongly developed, often slightly prominent, 1–1.5(–2) μm wide. *Hyphae* not studied. *Anamorph* not observed.

Hosts: Epiphyllous hepatics (Lejeuneaceae).

Known distribution: Costa Rica.

Bryocentria aequinoctialis is a necrotrophic parasite causing islet-like yellowish discoloured patches or lesions on its host. Döbbeler (2004) mentioned two additional collections from Costa Rica including a specimen from Cocos Island. At that time the species had not been formally described due to scantiness of material. A species similar to *B. aequinoctialis* was once observed while screening epiphyllous hepatics from Costa Rica. It differs by being a biotrophic parasite and having broadly ellipsoidal to almost globose ascospores. In Europe, there are two related necrotrophic *Bryocentria* species that also form superficial perithecia, but infect mosses. *Bryocentria cyanodesma* has larger perithecia, asci and ascospores, whereas *B. septinensis* deviates by slightly larger ascospores with delicate cyanophilous warts.

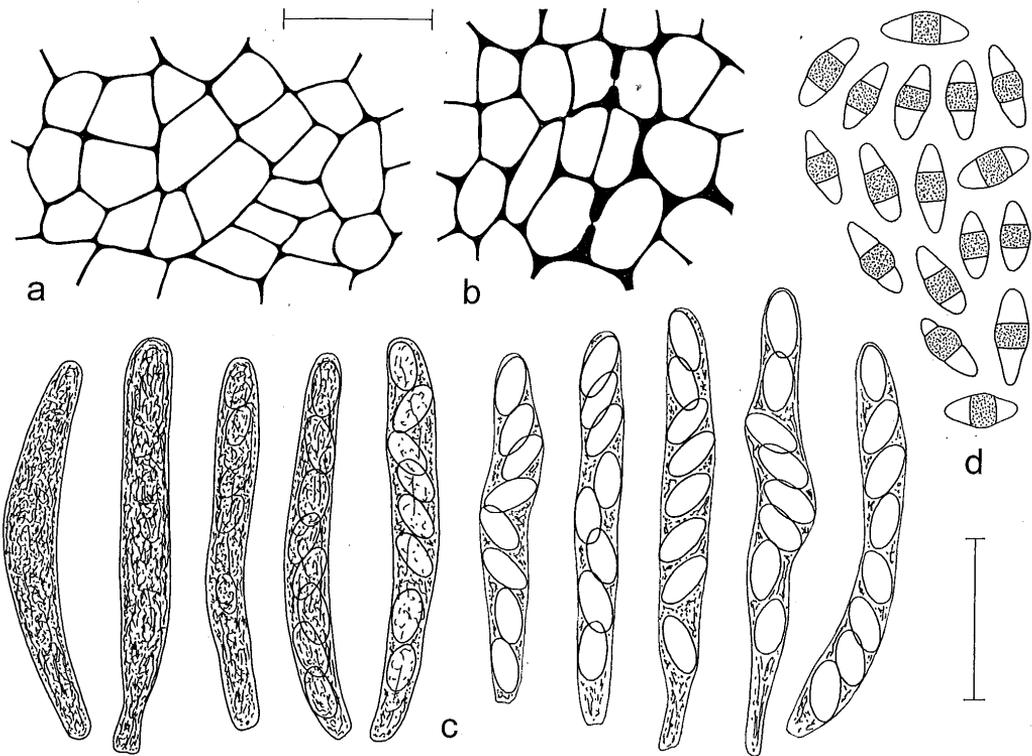


Fig. 1. *Bryocentria aequinoctialis*. a = excipulum seen from the outside, adjacent hyphae not drawn, b = as a, but cell walls pitted, c = asci: immature asci left, mature asci right, d = ascospores. – a, b, d holotypus; c Cocos Island. – a, b scale = 15 μm ; c, d scale = 10 μm .

Bryocentria brongniartii

Basionym: *Nectria brongniartii* P. Crouan & H. Crouan, Fl. Finistère 37. 1867. – *Bryocentria brongniartii* (P. Crouan & H. Crouan) Döbbeler, Mycol. Progr. 3: 248. 2004. Further synonyms, see Döbbeler (1978).

Perithecia leaf-perforating, globose to subglobose, orange-coloured, 140–220(–260) μm diam. *Excipulum* in surface view with 5–10(–15) μm wide cells, covered by 1.5–2.5 μm wide colourless hyphae. *Asci* more or less cylindrical, (31–)35–46(–55) \times 5–6(–7) μm . *Ascospores* dumbbell-shaped, colourless, two-celled, (6–) 6.5–7.5(–8) \times 2–2.5 μm (see Döbbeler 2004 for synonyms, detailed description including hyphal characters and illustrations).

Host: Frullania dilatata. *Known distribution: Ireland, England, Finland, Germany, Austria, Switzerland, France, Spain, Italy, Greece* (Döbbeler 2004); *Belarus, Portugal*. Priou (2008) gives many additional records from *France* and some from *Spain* and *Portugal*.

Byronectria brongniartii is a strictly host-specific biotrophic parasite. *Perithecia* develop on the protected ventral side of the leaves and perforate them. The ostioles are situated at the level of the dorsal leaf surface. In heavy infections single non-perforating *perithecia* may also be found between or upon leaves including the bracts of male inflorescences. Heavily infected plants with an elaborate white aerial mycelium on the ventral leaf side show a pale green discolouration. The species pertains to the most frequently encountered nectrioid ascomycetes on bryophytes.

Specimens examined: **BELARUS. Region Mogilev.** NW of Osipoviči, ca 160 m alt., 53°22'37" N, 28°22'26" E, 13.IX.2006 *Eckstein 6027* (M). **GERMANY. Bayern.** Oberbayern, Landkreis München, forest at the east-side of the river Isar, shortly southern of Grünwald, ca 550 m alt., 14.V.2005 *Döbbeler 8144* (M, TUR). Landkreis Starnberg, beginning of the Maisinger Schlucht, ca 630 m alt., 2.XI.2008 *Döbbeler 8653* (M); Maisinger Schlucht, ca 630 m alt., 14.XI.2004 *Döbbeler 8052* (TUR). Landkreis Bad Tölz-Wolfratshausen, Lenggries, parking area of the Brauneck-Bahn, ca 690 m alt., 25.VI.2005 *Döbbeler 8253* (TUR); Lainbachtal near Gschwendt, ca 670 m alt., 16.VII.2005 *Döbbeler 8276, 8277* (TUR). Landkreis Garmisch-Partenkirchen, Friedergriess shortly north of the custom office Griesen, 820–900 m alt., 2.X.2005 *Döbbeler 8308 & Schauer* (TUR); same location, 29.VII.2006 *Döbbeler 8483* (M). **FRANCE. Bretagne.** Morbihan, St. Martin, 24 m alt., 47°45'57" W, 02°14'59"

W, 18.V.2004 *Priou* (M). Vogesen, Benediktinerabtei Murbach, northwest Guebwiller, 7.VI.2008 *Döbbeler 8452* (M). **SPAIN. País Vasco.** Northeastern surroundings of Vitoria (Gasteiz), north side of Embalse de Ullibarri-Gamboa, ca 540 m alt., 23.VIII.2005 *Döbbeler 8351, 8360, 8362* (M); in the same region but southeast side of the lake, 8.VIII.2005 *Döbbeler 8332* (M), 8333 (TUR), 8339 (M), 8342 (TUR). **PORTUGAL.** Lindoso (border area to Spain). 41°52'19" N, 08°10'14" W, 374 m alt., 27. XII.2006 *Priou s. n.* (M). Trás-os-Montes, Geres, 41°41'43" N, 08°09'18" W, 533 m alt., 28.XII. 2006 *Priou 26232* (M). Beira Litoral, Praia de Cotegaca, Esmoriz, 40°55'50" N, 08°39'34" W, 16 m alt., 29.XII.2006 *Priou s. n.* (M); Praia de Vieira, 39°52'54" N, 08°57'49" W, 15 m alt., 30.XII.2006 *Priou 26233* (M).

Bryocentria cyanodesma

Bryocentria cyanodesma Döbbeler, Mycol. Progr. 3: 254. 2004.

Perithecia superficially formed on host leaves, ovoid or pyriform, orange-coloured, 200–280 \times 140–220(–250) μm , easily detached. *Excipular cells* seen from above 7–15(–20) μm wide. *Asci* cylindrical, 23–60 \times 4–5 μm . *Ascospores* almost cylindrical to narrowly ellipsoidal, colourless, two-celled, (5–)5.5–7.5(–8.5) \times 1.5–2(–2.5) μm , cyanophilous central part 0.5–1.5 μm wide, somewhat prominent (in lactophenol-cotton blue) (see Döbbeler 2004 for more details and illustrations).

Hosts: Grimmia pulvinata, Schistidium apocarpum, Tortella tortuosa. *Known distribution: Germany, Italy*.

The necrotrophic *Bryocentria cyanodesma* causes yellowish discolourations of the infected plants. *Perithecia* bearing shoots are not completely dead but may still have some green leaves or leaf parts.

***Bryocentria manubriata* Döbbeler sp. nov.**

– Fig. 2

MycoBank no.: MB518388

Etymology: Manubriatus (lat.) = having a hold; related to ascospore shape.

Perithecia superficialiter inter folia hospitis evoluta, subglobosa vel longiora quam latiora, flava vel incolorata, 150–200 \times 100–150 μm . Setae carentes vel sparsae, usque ad 20 μm longae. Ostiolum inconspicuum. Excipulum ca 15 μm crassum, cellulis rectangularibus, 5–11 μm

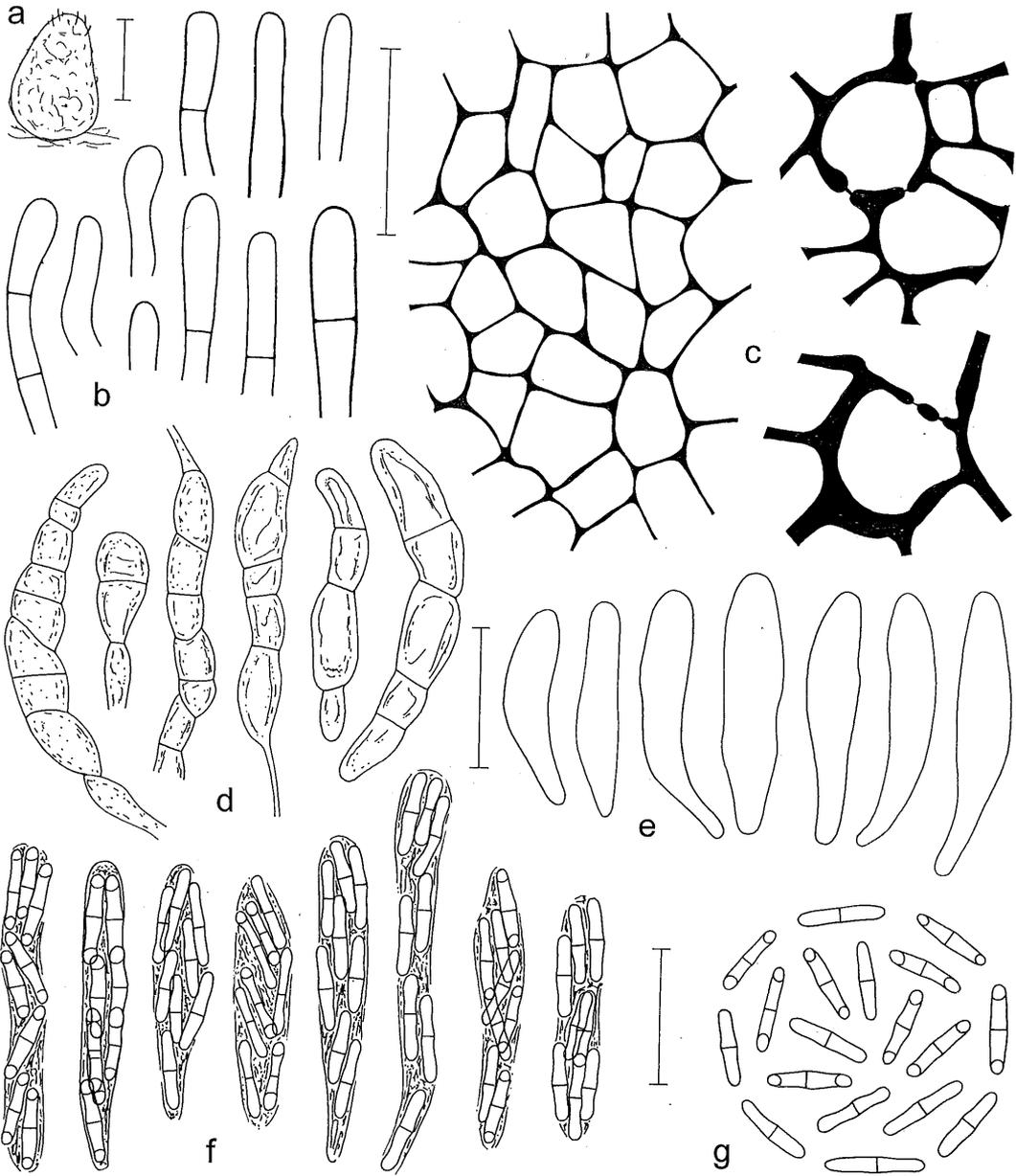


Fig. 2. *Bryocentria manubriata*. a = perithecium, b = setae, c = excipulum seen from the outside, adjacent hyphae not drawn, cell walls with pits (right), d = apical paraphyses e = immature asci in outline, f = mature asci, g = ascospores. – a, c (left), e *Döbbeler 8651*; c (right) *Döbbeler 8645*; b different collections; d holotypus; f, g *Döbbeler 8645*. – a scale = 100 μm ; b, c scale = 20 μm ; d–g scales = 15 μm .

largis, parietibus cyanophilis compositum, in superficie excipuli hyphae incoloratae praesentes; KOH ope non reagens. Paraphyses apicales mox dissolventes. Asci unitunicati, praecipue claviformes, 24–40 × 5–7 µm, octo-sporei, numerosi; reactio jodi negativa. Ascospores fere bacilliformes, utrinque rotundatae, bicellulatae, incoloratae, 8.5–10 × 2 µm, septo cyanophilo. Hyphae incoloratae, cyanophilae. Conidiomata non visa. Habitat parasitice in hepaticis epiphyllis familiae Lejeuneaceae laesiones decoloratas in hospite efficiens.

Typus: Costa Rica. Prov. Alajuela. Southern surroundings of the volcano Arenal, Parque Nacional Arenal, ca 600 m alt., 11.III.2008 Döbbeler 8652 (USJ – Holotypus).

Perithecia superficially formed, almost globose or distinctly longer than wide, colourless to yellowish, 150–200 × 100–150 µm. *Setae* absent or present in the uppermost part of the ascum, setae few, short, blunt, colourless, cyanophilous, up to 20(–27) µm long and 2.5–4.5(–5) µm wide. *Ostiole* inconspicuous, punctiform; ostiolar canal lined with filamentous periphyses. *Excipulum* ca 15 µm thick, composed of rectangular to rounded, rarely slightly undulate, cyanophilous, (3–)5–11(–18) µm wide cells, partly with up to 1.5(–2) µm wide pitted walls; surface loosely covered by adjacent hyphae; hyphae up to 25 µm long and 2–5 µm wide, cyanophilous; no colour change in KOH. *Apical paraphyses* extremely delicate, disappearing early. *Asci* unitunicate, mostly claviform, 24–40 × 5–7 µm, with delicate walls adjacent to the spores, walls at spore maturity hardly visible, eight-spored, without internal apical structures, numerous; iodine reaction (Lugol's solution) negative. *Ascospores* more or less rod-shaped with rounded ends, but thickest at the septum, at both ends normally also slightly enlarged, colourless, two-celled, (8–)8.5–10(–11) × 2 µm, often with a vacuole-like optically empty body at both ends, septum cyanophilous. *Hyphae* colourless, around perithecia 1.5–3 µm wide, cyanophilous. *Anamorph* not observed.

Hosts: Epiphyllous Lejeuneaceae, some perithecia also on intermingled thalli of *Metzgeria* sp. *Known distribution:* Costa Rica.

This new species grows necrotrophically, causing the dieback of its hosts. Infections, seen as bleached out or discoloured islet-like lesions on the hepatics, are dispersed within the cover of epiphyllae. Plants bearing ascumata are already

dead and show signs of decomposition. Different algae and detritus begin to accumulate. Perithecia develop on or between the leaves. They may also perforate the leaves from the ventral side, protruding distinctly. Within several months of collecting the perithecia are extremely difficult to detect. Having lost their yellowish colour they attain the same tint as the surrounding substrate.

Additional specimens examined: COSTA RICA. Prov. Alajuela. Southern surroundings of the volcano Arenal, Parque Nacional Arenal, ca 600 m alt., 11.III.2008 Döbbeler 8645, 8651 (M).

Bryocentria merospora Döbbeler sp. nov.

– Fig. 3

MycoBank no.: MB518389

Etymology: *Merosporus* (gr./lat.), *meros* = referring to parts or their number, *sporus* = related to spores; due to the disrupting ascospores.

Perithecia folia hospitis perforantia, globosa, aurantiaca usque ad flava, 140–170 µm diam. Setae carentes vel sparsae et valde breves. Ostiolum inconspicuum. Excipulum circa 10 µm crassum, cellulis rectangularibus vel rotundatis, 5–10 µm largis, parietibus cyanophilis compositum; superficie excipuli hyphis incoloratis obtecta; KOH ope non reagens. Paraphyses apicales fugaces. Asci unitunicati, subcylindrici, 22–34 × 3.5–4.5 µm, primo octo-sporei; reactio jodi negativa. Ascospores incoloratae, primum tricellulares et manipuliformes, 5–6 µm longae, 1–1.5 µm latae, ambae cellulae terminales globosae, cellula mediana bacilliformis; spores mox disrumpentes et duas sporas partiales inaequales formantes; spores partiales globosae denique in apicibus ascorum aggregatae. Hyphae non examinatae. Conidiomata non visa. Habitat parasitice in hepaticis epiphyllis familiae Lejeuneaceae laesiones decoloratas in hospite efficiens.

Typus: Costa Rica. Prov. Limón. Swamp forest near Tortuguero at the Caribbean coast, 10 m alt., 21.II.2007 Döbbeler 8621 (USJ – Holotypus).

Perithecia leaf-perforating, globose, golden yellow to yellowish, eventually colourless, 140–170 µm diam. *Setae* absent or sparsely distributed near the ostiole, up to 7 µm long, apically rounded. *Ostiole* inconspicuous, punctiform; ostiolar canal lined with periphyses. *Excipulum* ca 10 µm thick, composed of rectangular

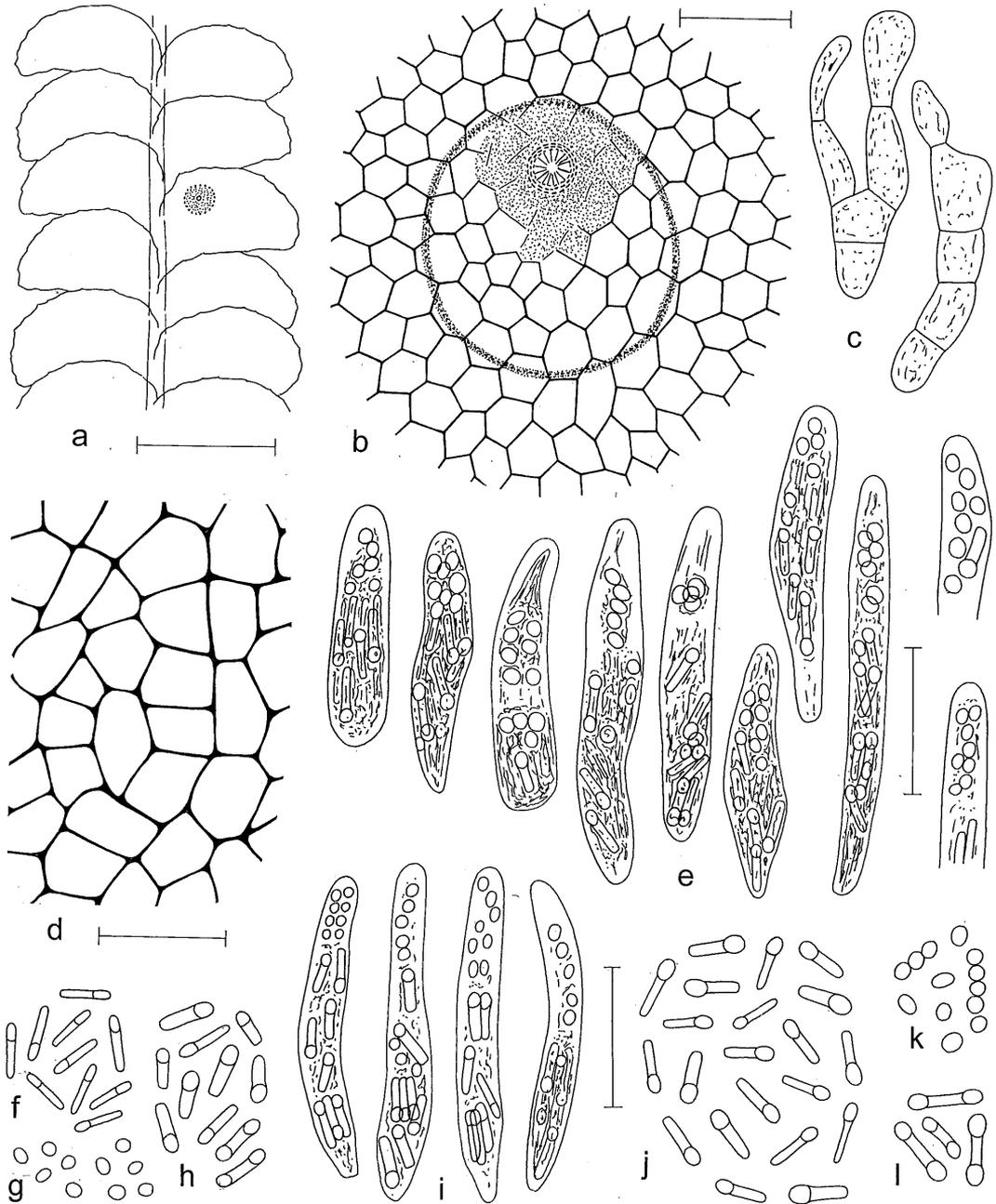


Fig. 3. *Bryocentria merospora*. a = infected plant with a leaf-perforating perithecium, dorsal view, b = as a, but drawn at higher magnification; the ostiole is level with the leaf cells, which are replaced at the perforation point by excipular tissue, c = apical paraphyses, d = excipulum seen from the outside, adjacent hyphae not drawn, e = mature asci, on the right two upper parts of asci, f–h = ascospores or parts of them: f = pin-shaped partial spores lying perpendicular to the plane, g = one-celled partial spores, h = partial spores lying in the plane, below two three-celled unbroken spores, i = mature asci, j–l = ascospores or parts of them: j = pin-shaped partial spores, k = one-celled partial spores, l = three-celled unbroken spores. – a, b, f–l *Döbbeler 8673*, c, d, e, j–l holotypus. – a scale = 7 mm; b scale = 60 μ m; c, e scale = 10 μ m; d scale = 15 μ m; f–l scale = 10 μ m.

to rounded, cyanophilous, 5–10(–15) μm wide cells; surface loosely covered by adjacent cyanophilous hyphae; no colour change in KOH. *Apical paraphyses* disappearing early. *Asci* unitunicate, mostly cylindrical or slightly enlarged in middle or lower part, apically rounded, (16–)22–34(–38) \times (3–)3.5–4.5(–5.5) μm , with delicate walls adjacent to the spores, walls at spore maturity hardly visible, at first eight-spored, without internal apical structures, at low magnification needle-shaped and very numerous; iodine reaction (Lugol's solution) negative. *Ascospores* colourless, in early developmental stages dumbbell-shaped, three-celled, 5–6 μm long, at both ends 1–1.5(–2) μm wide, one of the end-cells soon breaking off resulting in 16 dimorphic partial spores still lying in the ascus; pin-shaped partial spores two-celled, (3.5–)4–4.5(–5) μm long, globose cell 1–1.5(–2) μm diam, rod-shaped part about 1 μm wide, irregularly arranged within the asci, partly oriented to the ascus apex, partly to the base, rarely lying pairwise; separated globose or often slightly elongated partial spores one-celled, eventually concentrating in the apical ascus region (see also discussion below); spore walls apparently not cyanophilous; cytoplasmic content of the rod-shaped part generally slightly more cyanophilous than that of the globose part. *Hyphae* not studied. *Anamorph* not observed.

Hosts: Epiphyllous hepatics (Lejeuneaceae).

Known distribution: Costa Rica.

Bryocentria merospora is a necrotrophic parasite with unusual ascospores that distinguish this species in several regards. Disarticulating ascospores are a feature of widespread taxonomic distribution and well known in the Hypocreales (Rossman 1996, Rossman et al. 1999). Within the bryophilous fungi, *Nectria brenesii*, which is also parasitic on epiphyllous Lejeuneaceae, has two-celled spores that break off at the medium septum and form two almost equal partial spores (Döbbeler & Carranza 1993). *Bryocentria merospora*, however, has primarily three-celled, dumbbell-shaped ascospores with a septum at each end that separates two terminal globose cells. This early developmental stage seems to be a rapidly transient phase and disarticulation soon occurs. Usually, all spores of an ascus break off at the same time. The proximal or distal globose cell breaks off at the septum forming two dissimilar partial spores, one two-celled, pin-shaped

and asymmetrical, the other one-celled and globose. Such differently shaped ascospores within the same ascus are classed as dimorphic (Hyde et al. 1999). In this case the spore dimorphism is very pronounced. Separation of both globose cells of a single spore has not been observed.

The most curious phenomenon happens after disarticulation, namely the sorting out of the partial spores. The globose cells concentrate in the apical ascus region, forming an irregular group of up to eight cells (Figs. 3 e, i). Sometimes one or several isolated globose partial spores are still to be found in the middle or lower ascus region. In cases where only six or seven globose cells are situated in the apex, the missing cells must be further below or less than eight spores have been formed. Another explanation could be that a corresponding number of primary ascospores did not disarticulate. In many asci it is easy to count the apical cells, but impossible to recognize the exact number of spores in the middle or lower region because they are often clustered, lying one upon the other. Dimorphic partial spores that occupy different regions within an ascus seem to be unknown up to now.

A further peculiarity distinguishes the ascospores. Both the round end-cells and the central rod cell are, respectively, neither globose to ellipsoidal nor cylindrical structures but laterally compressed. Due to this unusual shape the two-celled partial spores can show different aspects depending on whether they lie in the plane or perpendicular to the plane (Figs. 3 f, h). The broad side is strongly preferred. Therefore to simplify matters the end-cells are described as globose even though discoid would be more correct.

A perithecium measuring 150 μm diam may contain at least 1500 asci. That means the formation of approximately 24000 diaspores if both the pin-shaped and the globose partial spores are fertile. Even if the globose partial spores function only as spermatia due to their smallness, fertility per fruit-body is astonishingly high and may explain why no asexual state is formed.

The new species is assigned to *Bryocentria* in spite of its unique spore characters. Ascoma size, shape and cellular structure of the excipulum, the reaction with lactophenol-cotton blue and the small and numerous formed asci and ascospores are features of all members of the genus. As described above, *B. merospora* deviates by having ascospores that disarticulate and the

resultant partial spores adopt an unique position within the asci. Their dumbbell-like shape before disarticulation is reminiscent of the spore form of *B. brongniartii*, the type species of the genus. However, the *B. brongniartii* ascospores are not easy to interpret regarding number of cells, and they show a cyanophilous reaction (Döbbeler 2004) that seems to be absent in *B. merospora*. As the cytoplasmatic content touching the cell wall gives a positive cotton blue-reaction, the colouration of the cell wall is hard to evaluate in extremely small spores.

Additional specimens examined: COSTA RICA. Prov. Limón. Parque Nacional Braulio Carrillo, Sendero “Quebrada Gonzales” near the station in the lowermost part of the park, 540–600 m alt., 5.III.2008 *Döbbeler 8673* (M). **Prov. Alajuela.** Eastern slope of the Cordillera de Tilarán, Reserva Biológica Alberto Manuel Brenes, surroundings of the Biological Station of the Universidad de Costa Rica at the Río San Lorencito, 850–950 m alt., 1.III.2007 *Döbbeler 8632* (M).

Bryocentria metzgeriae

Basionym: *Pseudonectria metzgeriae* Ade & Höhn., in Höhnel 1919, Ann. Mycol. 17: 117. – *Bryocentria metzgeriae* (Ade & Höhn.) Döbbeler, Mycol. Progr. 3: 252. 2004.

Perithecia leaf-perforating, globose to subglobose, orange-coloured, (150–)170–230(–270) µm diam, the disk-like apex sometimes surrounded by few short setae. *Excipulum* in surface view with (5–)7–15(–20) µm wide cells, loosely covered by (1.5–)2–3(–4) µm wide colourless hyphae. *Asci* cylindrical or clavate, 28–50(–65) × (4–)4.5–5.5(–6) µm. *Ascospores* fusiform, colourless, two-celled, (4.5–)5.5–7.5(–8.5) × 1.5–2(–2.5) µm (see Döbbeler 2004 for a synonym, detailed description including hyphal characters and illustrations).

Hosts: *Frullania dilatata*, *Lejeunea cavifolia*, *Metzgeria furcata*, *Porella platyphylla*, *Porella* sp., *Radula complanata* (most frequent host). *Known distribution:* Germany, Austria, Switzerland, France, Spain, Croatia, Greece (Döbbeler 2004).

Bryocentria metzgeriae kills its hosts, the infection causing discoloured, yellowish, irregular spots of varying size within green and healthy mats. Infected leaves tend to stick together showing signs of incipient decomposition. Leaf

perforation occurs as in *B. brongniartii*. Almost all host species grow on bark of trees.

Specimens examined: GERMANY. Bayern. Oberbayern: Landkreis München, forest at the east-side of the river Isar, shortly southern of Grünwald, ca 550 m alt., on *Radula complanata*, 14.V.2005 *Döbbeler 8143* (M, TUR). Landkreis Starnberg, beginning of the Maisinger Schlucht, ca 630 m alt., on *R. complanata*, 2.XI.2008 *Döbbeler 8654* (TUR); same location, on *Metzgeria furcata*, *R. complanata*, 14.XI.2004 *Döbbeler 8051* (M). Landkreis Miesbach, Taubenberg, 670 m alt., on *R. complanata*, 12.XI.2005 *von Brackel s. n.* (M). Landkreis Bad Tölz-Wolfratshausen, Lainbachtal near Gschwendt, ca 670 m alt., on *R. complanata*, 16.VII.2005 *Döbbeler 8279* (M); same location and date, on *M. furcata*, *R. complanata*, *Döbbeler 8278* (TUR); Walchensee, southeast lakeside, on *R. complanata*, 780 m alt., 1.XI.2006 *von Brackel & von Brackel 3876* (M). Landkreis Garmisch-Partenkirchen, Friedergriess shortly north of the custom office Griesen, 820–900 m alt., on *R. complanata*, 2.X.2005 *Döbbeler 8311 & Schauer* (TUR).

Bryocentria septinensis Döbbeler sp. nov.

– Fig. 4

Mycobank no.: MB518390

Etymology: Artificial name containing the first syllable of *Seppo* and the last two syllables of *Huhtinen*. Named in honour of Dr. Seppo Huhtinen (Turku).

*Perithecia superficialiter in foliis et caulibus hospitis evoluta, pyriformia ad conica vel ovoidea, in statu vivo aurantiaca, mox incolorata, 120–170 × 90–150 µm, apicaliter plerumque setis brevibus ornata. Excipulum hyphis incoloratis plus minusve densis obtectum. Parietes excipuli e stratis nonnullis cellularum rectangularum compositus, externe visus cellulis angulatis, cyanophilis, 6–10 µm diametentibus praeditus; KOH ope non reagens. Asci unitunicati, cylindrici, parietibus evanescentibus, ca 45 × 5 µm, octo-sporei; reactio jodi negativa. Ascosporae doliiformes, incoloratae, bicellulatae, leviter verrucosae, 6–7 × 3–3.5 µm, pars centralis cingulo cyanophilo ornata. Hyphae incoloratae, cyanophilae, 1.5–3 µm latae. Conidiomata vel conidia non visa. Habitat parasitice in foliis decoloratis et emortuis musci *Sanionia uncinata*.*

Typus: **Finland. Pohjois-Häme.** Woodland about 11 km SSW of Suolahti, grid 27° E 6929-6931: 435-436, 10.IX.2004 *Döbbeler 8179 & Huhtinen* (TUR – holotypus; M – isotypus).

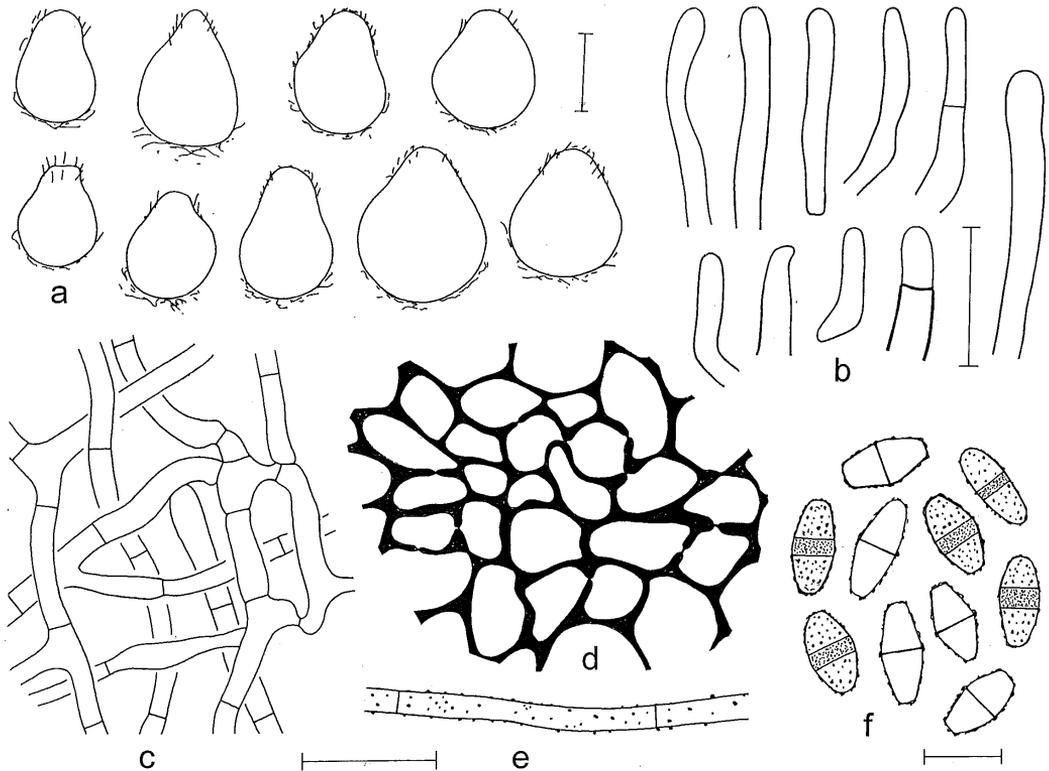


Fig. 4. *Bryocentria septinensis*, holotypus. a = perithecia in outline, b = setae, one of them showing apical regeneration, c = hyphae overlying excipular cells, d = excipular cells with pitted walls seen from above, overlying hyphae not drawn, e = hypha with cyanophilous warts, f = ascospores with cyanophilous warts, seen from above with cyanophilous band or in optical section. – a scale = 90 μm ; b–e scales = 15 μm ; f scale = 5 μm .

Perithecia superficially formed on infected plants, pyriform to conical or ovoid, orange-coloured when fresh but soon bleaching (completely colourless after about two years), 120–170 \times 90–150 μm , with few to many short apical setae. *Setae* colourless, cylindrical, rounded, aseptate or rarely with one septum, sometimes annularly surrounding the ostiolar region, up to 20(–35) μm long and 2.5–4 μm wide, with cyanophilous walls. *Ostiole* inconspicuous; periphyses lining the ostiolar canal. *Ectal excipulum* composed of several layers of rectangular, ca 8 μm wide cells; cells seen from above often indistinct, angular or with slightly undulate, irregularly thickened, cyanophilous and sometimes pitted walls, in the middle and lower part 6–10(–15) μm wide; excipulum covered with a thin web of adjacent, cyanophilous, 2–4 μm wide hyphae; no colour change in KOH. *Apical paraphyses* not seen. *Asci* unitu-

nicate, cylindrical, disappearing early, ca 45 \times 5 μm , eight-spored; iodine reaction (Lugol's solution) negative. *Ascospores* doliiform, colourless, two-celled, (5.5–)6–7 \times 3–3.5(–4) μm , uniseriate within the asci, episporium usually with delicate, cyanophilous warts, rarely apparently smooth, the septal region surrounded by an inconspicuous, cyanophilous, up to 2 μm wide band. *Hyphae* colourless, thin-walled, ramified, 1.5–3 μm wide, sometimes more or less densely covered with cyanophilous warts, intracellular hyphae also present. *Anamorph* not observed.

Host: *Sanionia uncinata* (syn. *Drepanocladus uncinatus*). *Distribution*: Known only from the type collection.

Bryocentria septinensis (Bionectriaceae, Hypocreales) is a necrotrophic parasite. It causes a conspicuous yellowish discolouration of the infected host plants, which subsequently

die off. Signs of decomposition are not visible during fruit-body formation. The perithecia occur sparsely on the surface of dead host leaves and shoots, mostly in a region 2 to 8 mm below the apex. Only one or very few leaves of a shoot normally harbour perithecia, although two may develop on the same leaf. They are often laterally attached or can even be connected by a small aerial hyphal web between two adjacent leaves. In contrast to several non-leaf-perforating nectrioid species with easily detachable perithecia, in *B. septinensis* the perithecia adhere rather firmly to the substrate.

The new species is characterized by small orange-coloured perithecia, web-like hyphae covering the angular, pitted excipular cells, the formation of short setae, and two-celled, barrel-shaped ascospores with tiny warts and a band-like transverse structure. The cyanophilous reaction of the cell walls of hyphae including their septa, excipular cells and the epispore is very conspicuous. At least some hyphae bear cyanophilous warts on their surface.

Bryocentria septinensis is well placed in the genus *Bryocentria*. An important generic character is that the very small two-celled ascospores are encircled by a cyanophilous band (Döbbeler 2004), which is best seen stained with lactophenol-cotton blue and using phase-contrast optics. *Bryocentria septinensis* seems to be most closely related to *B. cyanodesma*, which also grows necrotrophically on various acrocarpous mosses in Europe. The species differ mainly in their ascospore features: the ascospores of *B. cyanodesma* are almost cylindrical to narrowly ellipsoidal and are only 1.5–2 µm wide, as opposed to the doliiform ascospores of *B. septinensis*, which are typically twice the width.

Discussion

The species assigned to the genus *Bryocentria* differ considerably with regard to their ascospore characters, host selection, ecology, and geographical occurrence. The biotrophic *B. brongniartii*, the only *Bryocentria* species apparently living in equilibrium with its host, and the necrotrophic *B. metzgeriae* seem to be closely related although the form of parasitism is quite different. Both have comparable ascospores and perforate

the host leaves from the ventral side. They infect corticolous hepatics in Europe and can occur on the same phorophyte. Recently their phylogenies confirmed the affinity to Bionectriaceae (Stenroos et al. 2010)

A second group comprises *B. aequinoctialis*, *B. cyanodesma*, and *B. septinensis*. These species have the same spore type characterized by a central cyanophilous band-like structure. They all form superficial ascomata but colonize systematically and ecologically diverse hosts. *Bryocentria aequinoctialis* parasitizes epiphyllous Lejeuneaceae in tropical rain forests, whereas both other species grow on mosses in Europe.

The two remaining species *B. manubriata* and *B. merospora* also occur as hyperepiphylls on Lejeuneaceae but differ by ascospore features. Further studies will reveal if *Bryocentria* is homogeneous. At present it is also unclear whether the two related species *Nectria gynophila* and *N. perianthicola*, which develop within the perianths of the epiphyllous *Radula flaccida* (Döbbeler 2010), belong to *Bryocentria*.

Biologically, *Bryocentria* is remarkable as almost all its members behave as highly efficient necrotrophs. Typically, bryophilous taxa do not alter the aspect of their hosts in any visible manner. No asexual state has been observed in any of the *Bryocentria* species. Instead, infection stress exerted by the ascospores alone seems to be adequate. They are extremely small and produced in great numbers per perithecium, overwhelming the host tissues.

Although discoloured bryophytes within a green mat or cushion are highly visible and attract the observer's attention in the field, few collections were available for this study. The muscicolous species seem to be genuinely rare and are not merely rarely collected. Hyperepiphyllous Hypocreales are more frequent and undiscovered taxa surely exist. Only a limited number of phorophyte leaves with epiphyllae could be screened for this study. Nevertheless, *Bryocentria* and its newly described species represent the increasing number of nectrioid fungi recorded as parasites on bryophytes, especially on those of the phyllosphere. They seem to reflect the explosive evolution and enormous diversification of their lejeuneaceous hosts (Schuster 1980) resulting in fungi with hitherto unrecorded features.

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