A monograph of *Bionectria* (Ascomycota, Hypocreales, Bionectriaceae) and its *Clonostachys* anamorphs

Hans-Josef Schroers

Centraalbureau voor Schimmelcultures, Fungal Biodiversity Centre, P.O. Box 85167, NL-3508 AD Utrecht, The Netherlands

Abstract: Species of the genus *Bionectria* (*Hypocreales*, *Bionectriaceae*) with anamorphs in *Clonostachys* are reviewed. *Bionectria* is distinct from other genera of the *Bionectriaceae* in overall shape and septation of the ascospores, ascus morphology, ecology, and, in particular, characters of the anamorph. Several other characters of the ascomata may differ from those seen in other genera of the *Bionectriaceae* as well but none of these is consistently formed in all *Bionectria* species. The understanding of this genus necessitates emphasis on character patterns rather than single features, because certain characters may overlap with those of other nectrioid taxa. *Bionectria* forms a monophyletic clade based on analyses of the partial large subunit of the ribosomal DNA (LSU rDNA). The genus includes destructive mycoparasites, some of which are used as biocontrol agents of fungal plant pathogens, as well as species with other substrate associations.

The teleomorphs of *Bionectria* are classified in the six newly distinguished subgenera ***Bionectria***, ***Zebrinella***, ***Astromata***, ***Myronectria***, ***Epiphloea***, and ***Uniparietina***, based on stroma morphology, stroma–perithecium wall interface structure, perithecial wall anatomy, habit of the perithecia on the natural substratum, and ascospore ornamentation and septation. Some but not all of the morphologically delimited subgenera are paraphyletic based on sequences of the internal transcribed spacer regions of the rDNA (ITS rDNA) and a portion of the β-tubulin gene (*tub*2).

The anamorphs of *Bionectria* are classified in *Clonostachys*. After reinterpretation of some characters, heightened emphasis on overall character patterns, consideration of transition series within particular character states, and consideration of the appearance of colonies both on the natural substratum and in pure culture, *Clonostachys* is broadly delimited to include anamorphs formerly classified in *Verticillium*, *Gliocladium*, *Acrostalagmus*, *Sesquicillium*, *Spicaria*, *Dendrodochium*, *Clonostachyopsis*, *Verticilliodochium*, *Gliocladochium*, and *Myrothecium*. All taxa of *Bionectria* are united by phenotypic characters of the anamorph such as penicillate conidiophores, conidia held in

imbricate columns, and predominantly more or less curved conidia with mostly laterally displaced hila. These characters are rare or not formed in other genera of the *Bionectriaceae*. Conidiomata, intercalary phialides, conidiophore dimorphism, and conidial mass colour are variable within *Bionectria*, although to a certain extent they may reflect subgeneric affinities.

In *Bionectria* / *Clonostachys* 44 holomorphic or anamorphic species are distinguished based on morphological discontinuities. Based on inferences from ITS rDNA and *tub*2 sequences, most of the species form monophyletic units. In few cases paraphyletic clades are accepted as species. In two species, *C. rosea* and *C. solani*, infraspecific forms are proposed to segregate strains with either white to pale orange or green conidial masses.

The following taxa are accepted, newly combined (bold letters, *comb. nov.*), or newly described (bold letters: *subgen. nov.*, *sp. nov.*, or *stat. nov.*): Subgenus *BIONECTRIA*: *B. apocyni*/***C. macrospora*** *comb. nov.* – ***B. aureofulvella*** *sp. nov.*/***C. aureofulvella*** *stat. nov.* – *B. byssicola*/***C. byssicola*** *stat. nov.* – ***B. capitata*** *sp. nov.*/***C. capitata*** *stat. nov.* – ***B. compactiuscula*** *sp. nov.*/*C. compactiuscula* – ***B. kowhaii*** *comb. nov.*/***C. kowhaii*** *stat. nov.* – ***B. oblongispora*** *sp. nov.*/***C. oblongispora*** *stat. nov.* – *B. ochroleuca*/*C. rosea* – *C. rosea* f. ***catenulata*** *stat. nov.* – ***B. zelandiaenovae*** *sp. nov.*/***C. zelandiaenovae*** *stat. nov.* – ***B. pseudochroleuca*** *sp. nov.*/***C. pseudochroleuca*** *stat. nov.* – ***B. pseudostriata*** *sp. nov.*/***C. pseudostriata*** *stat. nov.* – ***B. ralfsii*** *comb. nov.*/***C. ralfsii*** *stat. nov.* – ***B. samuelsii*** *sp. nov.*/***C. samuelsii*** *stat. nov.* – ***B. solani*** *comb. nov.*/***C. solani*** *comb. nov.* – *C. solani* f. ***nigrovirens*** *stat. nov.* – ***B. sporodochialis*** *sp. nov.*/***C. sporodochialis*** *stat. nov.* – *B. tonduzii*/*C.* ?*macrospora* – ***B. verrucispora*** *sp. nov.*/***C. verrucispora*** *stat. nov.* – ***C. agrawalii*** *comb. nov.* – ***C. divergens*** *sp. nov.* – ***C. rhizophaga*** *sp. nov.* – ***C. rogersoniana*** *sp. nov.* – Subgenus ***ZEBRINELLA*** *subgen. nov.*: ***B. grammicospora*** *comb. nov.*/***C. grammicospora*** *stat. nov.* – ***B. grammicosporopsis*** *comb. nov.*/***C. grammicosporopsis*** *stat. nov.* – ***B. levigata*** *sp. nov.*/***C. levigata*** *stat. nov.* – ***B. lucifer*** *comb. nov.*/***C. lucifer*** *stat. nov.* – ***B. subquaternata*** *comb. nov.*/***C. subquaternata*** *stat. nov.* – ***C. chlorina*** *sp. nov.* – ***C. intermedia*** *sp. nov.* – Subgenus ***ASTROMATA*** *subgen. nov.*: ***B. epichloë*** *comb. nov.*/***C. epichloë*** *stat. nov.* – ***B. parva*** *sp. nov.*/?*C. miodochialis* – ***C. miodochialis*** *sp. nov.* – Subgenus ***MYRONECTRIA*** *subgen. nov.*: ***B. pityrodes*** *comb. nov.*/***C. pityrodes*** *stat. nov.* – Subgenus ***EPIPHLOEA*** *subgen. nov.*: ***B. gibberosa*** *sp. nov.*/*C.* cf. *setosa* – ***B. impariphialis*** *comb. nov.*/***C. impariphialis*** *comb. nov.* – ***B. lasiacidis*** *comb. nov.*/***C. lasiacidis*** *stat. nov.* – ***B. parviphialis*** *comb. nov.*/***C. pseudosetosa*** *comb. nov.* – ***B. rossmaniae*** *sp. nov.*/***C. rossmaniae*** *stat. nov.* – ***B. sesquicillii*** *comb. nov.*/***C. sesquicillii*** *stat. nov.* – ***B. setosa*** *sp. nov.*/***C. setosa*** *comb. nov.* – ***B. tornata*** *comb. nov.*/***C. asymmetrica*** *comb. nov.* – ***C. candelabrum*** *comb. nov.* – ***C. phyllophila*** *sp. nov.* – Subgenus ***UNIPARIETINA*** *subgen. nov.*: *B. aurantia* – ***B. coronata*** *comb. nov.*/***C. buxi*** *comb. nov.*

INTRODUCTION

Spegazzini (1919) proposed the genus *Bionectria* for species of *Nectria* Fr. that occur on living plant material. He originally included one species based on a single specimen, which was characterized by flesh-coloured to orange perithecia crowded on a well-developed stroma, and fusiform, apically rounded asci with 1-septate ascospores.

Subsequent authors considered *Bionectria* a synonym of *Nectria*. This was for several reasons: First, the only described species, *B. tonduzii* Speg., was never recollected and the genus remained generally obscure. Second, the plant-parasitic life style was not considered a significant character for generic delimitation in hypocrealean fungi (Weese, 1927; Müller & von Arx, 1962; Samuels, 1988a). Third, *Nectria* was generally broadly circumscribed, particularly by authors of the 20th century. Based on relatively few characters such as brightly coloured, stromatous or astromatous perithecia, unitunicate asci, and mostly 1-septate ascospores, more than 700 species were eventually included.

Today, *Nectria*-like species are distributed over at least 52 genera that are divided into three families of the *Hypocreales*, the *Hypocreaceae*, the *Nectriaceae* and the recently established *Bionectriaceae* (Rossman *et al*., 1999), of which *Bionectria* is the type genus. *Nectria* itself is restricted to less than 30 species related to the type species, *N. cinnabarina* (Tode : Fr.) Fr. (Rossman, 1989). The generic delimitations proposed (Rossman *et al*., 1999) take into account the habit and life-style of the fungi, character patterns of the ascocarps, phylogenies inferred from DNA sequences as far as available (Rehner & Samuels, 1995; Rossman *et al*., 2001), and life cycle studies. The emerging taxonomy conforms to the dictum that the category of a genus should comprise monophyletic groups of species.

The recognition of naturally related species groups in hypocrealean fungi is largely based on similarities among anamorphs (Samuels & Seifert, 1987). Even more than those of the teleomorphs, however, anamorph genera frequently are broadly delimited. Some have been refined after re-examination and reinterpretation of certain character patterns (Seifert, 1985), particularly if these could be correlated to certain teleomorphs or DNA-based phylogenies (e.g. Glenn *et al*., 1996, for *Epichloë* (Fr.) Tul. & C. Tul. / *Neotyphodium* Glenn *et al*.). Similarly, the anamorph of *Bionectria ochroleuca* (Schw.) Schroers & Samuels was classified in *Clonostachys* Corda as *C. rosea* (Link : Fr.) Schroers *et al*. (1999b) (≡ *Penicillium roseum* Link : Fr., = *Gliocladium roseum* Bain.). This transfer from *Gliocladium* Corda to *Clonostachys* took into account (i) different morphologies of the conidiophores of the respective type species, *C. araucaria* (Corda, 1839) and *G. penicillioides* (Corda, 1840), (ii) morphological differences of their respective teleomorphs, *B. ochroleuca* and *Sphaerostilbella aureonitens* (Tul.) Seifert, Samuels & W. Gams, (iii) phylogenies derived from sequence data showing that the species belong to different families (Rehner & Samuels, 1994, 1995), and (iv) different life-styles and substrata, viz. destructive mycoparasitism, soil, recently dead trees, etc. for *B. ochroleuca*/*C. rosea*, and fungicolous growth on aphyllophoralean fungi or rotten wood for *S. aureonitens*/*G. penicillioides*. The recognition of *Bionectria* and its link to *Clonostachys* is based on similarities between perithecia of *B. tonduzii* and *B. ochroleuca* and related species, whose life cycle were studied (Dingley, 1957; Smalley & Hansen, 1957; Booth, 1959; Samuels, 1976a). No anamorph has ever been linked to *B. tonduzii*.

The anamorphs of species in *Bionectria* are characterized by penicillate, frequently sporodochial, and, in many cases, dimorphic conidiophores (referred to here as the primary and secondary conidiophores). The secondary conidiophores generally form imbricate conidia that can collapse to slimy masses, particularly on sporodochia. Various colours of the conidial masses such as white, pale orange, or green have been observed (Domsch *et al*., 1980). The primary conidiophores were first described by Bainier (1905, 1907b). They are mononematous, either verticillium-like or narrowly penicillate, and form heads of watery conidial masses. Species that were mainly based on primary conidiophores were classified in *Verticillium* Nees; those based on secondary conidiophores were classified in *Clonostachys*, *Gliocladium*, *Acrostalagmus* Corda, *Sesquicillium* W. Gams, and *Clonostachyopsis* Höhn.; those mainly based on sporodochia in *Spicaria* Harting, *Dendrodochium* Bonorden, *Verticilliodochium* Bubák, as *Myrothecium* sp., ?*Tubercularia* Tode, and *Gliocladochium* Höhn.

While it is certain that *Clonostachys* is the appropriate genus for anamorphs of *Bionectria*, species delimitation based on morphological characters of the conidiophores is difficult. Considerable variation is found in the branching patterns of primary and secondary conidiophores, tendencies towards sporodochium formation, frequencies of intercalary phialides, overlapping size ranges of conidia, growth rates in vitro, and macroscopic characters such as colony pigmentation. These character variations suggest that taxa described in *Clonostachys* or *Gliocladium*, respectively, present species complexes rather than easily defined units. A similar degree of variation is also seen in teleomorph characters such as size ranges of ascospores as well as the colour, surface structures, and growth habit of the perithecia. This may render identification at species level difficult.

Here a revision of the genus *Bionectria*/*Clonostachys* is presented based on conidial isolates, strains isolated from ascospores, and numerous herbarium

specimens of *Bionectria*-like ascocarps with or without correlated strains. The goal of the study was to observe whether discontinuities in the teleomorphs could be correlated with those in the anamorphs, to delimit species based on the holomorph, and to integrate strains and species only known as anamorphs in the holomorphic system. For the identification of species, decisions on synonymy, and segregations of undescribed taxa, the characters obtained were compared with those of relevant type specimens and of published descriptions. Most known taxa are redescribed and some are newly described. In addition to *Bionectria* in the sense of Schroers & Samuels (1997) and Rossman *et al*. (1999), species of the '*Nectria*' *grammicospora*-group (Samuels, 1988b), the '*N.*' *sesquicillii*-group (Samuels, 1989), a few species of the '*N.*' *ralfsii*-group (Rossman, 1983), and some related species are included in *Bionectria* (see also Schroers, 2000). The taxonomic scheme proposed, takes into account a phylogeny inferred from sequences of the nuclear ribosomal DNA and the *tub*2 gene.

HISTORICAL OVERVIEW

CLASSIFICATION OF TELEOMORPHS AND HOLOMORPHS

The distinction of naturally related groups at higher taxonomic levels is mainly based on distinct types of the ascocarp centrum development (reviewed by Miller, 1949). Luttrell (1951) thoroughly described the different developmental types of the pyrenomycetes and redefined the *Hypocreales* G. Lindau as having unitunicate asci and a *Nectria*-type centrum development. This type is defined by downward-directed apical paraphyses that disappear prior to maturity and asci arising mainly from the base of the centrum. Rogerson (1970) adopted this concept and accepted a single family in the *Hypocreales*, the *Hypocreaceae*, characterized by fleshy, generally brightly coloured, superficial or immersed (in a stroma or substratum), stromatous or astromatous perithecia, well-developed perithecial walls, and mostly phialidic anamorphs. Rossman *et al*. (1999) reviewed the genera of the *Hypocreales* and distinguished three families: (1) *Hypocreaceae* (12 genera), characterized by often disarticulating ascospores and perithecia that are mostly immersed in a stroma or seated on a subiculum; (2) *Nectriaceae* (20 genera), characterized by non-fragmenting ascospores and immersed or mostly superficially free, red perithecia that generally turn purple or more intensely red in KOH and pale again after addition of lactic acid (positive KOH reaction); (3) *Bionectriaceae* (26 genera), characterized by non-fragmenting ascospores and immersed or mostly superficially free, pale, whitish, orange, or brown perithecia that do not react in KOH or lactic acid (negative KOH reaction). The distinction of the families also receives support from cladistic analyses of LSU rDNA sequences (Rehner & Samuels, 1995; Rossman *et al*., 2001). Although clavicipitalean fungi have a distinct type of perithecium development (White, 1997), they are included in the *Hypocreales* based on molecular data (Glenn *et al*., 1996; Spatafora & Blackwell, 1993). Although not yet supported by molecular data, the *Niessliaceae* are also considered close relatives. Among other ascomycetes, the *Hypocreales* are related to the *Microascales*, *Xylariales*, *Sordariales*, and *Diaporthales* (Sugiyama, 1998; Suh & Blackwell, 1999) that all belong to the class *Sordariomycetes* O. Eriksson & Winka.

Species with free perithecia or with structures resembling perithecia were first classified in *Sphaeria* Haller 1768. The earliest record of a *Bionectria* species is *Sphaeria ochroleuca* described by Schweinitz (1834) [1832]. *Sphaeria* was rejected in favour of the younger genus *Hypoxylon* Bull. after discussions about its typification (Donk, 1964). Fries (1825) described *Nectria* as an infrageneric section of *Hypocrea* Fr. for species with perithecia formed superficially on a subiculum, a tomentose matrix, or directly seated on the substratum. Fries (1849) raised the section to generic level and gave additional characters such as the bright colour of the perithecia, 8-spored asci, and hyaline ascospores. Saccardo (1878) restricted the genus to species with 1-septate ascospores. Among numerous other species, he accepted three species now classified in *Bionectria*, *N. pityrodes*, *N. ralfsii*, and *N. subquaternata*.

Later, Saccardo (1883, 1895), and Saccardo & Saccardo (1905) rearranged *Nectria*-like species in 10 subgenera distinguished according to the presence or absence and nature of a stroma or subiculum, perithecial surface structures, and ascospore morphology. Some species now classified in *Bionectria* were placed in the subgenera *Hyphonectria* (type species *Hydropisphaera peziza* (Tode : Fr.) Dumort.), characterized by perithecia seated on a byssoid stroma or subiculum (*N. by*ssicola), *Eu-Nectria*, characterized by perithecia seated on a well-developed stroma (*N. aureofulva*, *N. subquaternata*), or *Lepidonectria* characterized by warted perithecia (*N. ralfsii*, *N. apocyni*, and *N. pityrodes*), or they remained unclassified. These subgenera were raised to generic rank by Cooke (1884) and were partly accepted by others. Today only one of Saccardo's subgenera, *Lasionectria* (Sacc.) Cooke, is accepted as a genus in the *Hypocreales*, while the others were placed in synonymy with older genera.

Kuntze (1898) transferred the species classified at that time in *Nectria* into the older genus *Cucurbitaria* Gray (1821) because the majority of Gray's original species had been accepted in *Nectria* by Fries (1849). Kuntze ignored the identity of the type species of *Cucurbitaria*, *C. berberidis* (Pers.) Gray, which is well understood and has been used by numerous subsequent authors as the type of the dothidealean genus *Cucurbitaria* (e.g. Mirza, 1968).

Seaver (1909 a, b) used two subfamilies, *Nectrieae* centred on *Nectria* for species without and *Creonectrieae* on *Creonectria* Seaver for species with a well-developed stroma. Seaver (1909a) regarded *Sphaeria peziza* Tode : Fr. as the lectotype of *Nectria* and (1909b) *Tremella purpurea* L. (= *Nectria cinnabarina*) as the lectotype of *Creonectria*. Representatives of *Bionectria* were classified in *Nectria* or *Creonectria* (Seaver, 1909ab). His lectotypifications were not accepted.

Clements & Shear (1931) presented a hierarchy of taxa in the schematic tradition of Saccardo. Within the artificial order *Sphaeriales*, they recognized one family, the *Hypocreaceae*, that also contained some genera today classified in the *Clavicipitaceae*. They lectotypified *Nectria* with *N. cinnabarina* (Tode : Fr.) Fr. and characterized it by 1-septate, hyaline ascospores, 8-spored asci, superficial perithecia, and as being non-lichenicolous. According to the keys provided by Clements and Shear (1931), most species of *Bionectria* could be classified in *Nectria*.

Nectria (Fr.) Fr. 1849 was conserved against Dumortier's genera *Ephedrosphaera* 1822 and *Hydropisphaera* 1822 (Cannon & Hawksworth, 1983). Because *Hydropisphaera* originally contained only one species, *H. peziza* (Tode : Fr.) Dumort., it is available as the oldest genus for the *Nectria peziza*-group (Samuels, 1976a; Rossman *et al*., 1999) that includes species with astromatous, smooth perithecia that sometimes are covered with fringes of hyphae, and acremonium-like anamorphs. *Hydropisphaera* is closely related to *Bionectria* (Rossman *et al*., 2001).

Other 20th century authors focused on patterns of characters but accepted a rather broadly delimited genus *Nectria*. Weese clearly understood his contributions as the grandwork necessary to attain the goal of a phylogenetic classification system [1916, p. 465: "... und doch ist noch eine reiche Fülle von Kleinarbeit zu vollbringen, bis (...) man (...) an die Aufstellung eines (...) neuen Systems nach phylogenetischen Gesichtspunkten (...) wird schreiten können"]. Weese generally would not accept descriptions of new genera before existing genera were comprehensively reviewed (Weese, 1916, 1927). In contrast to previous authors, he emphasized the importance of perithecial wall anatomy and included the colour reaction of ascocarps in KOH as a descriptive character. Later, this colour reaction was used to segregate otherwise similar taxa (Samuels *et al*., 1990) and to segregate the *Bionectriaceae* from the *Nectriaceae* (Rossman *et al*., 1999).

The discovery of pleomorphic life cycles by De Bary (1854) and Tulasne & Tulasne (1861) led to the acceptance of a dual or anatomical classification system (Fuckel, 1870) and not to a classification based on both morphs jointly. However, at least at the species level, connections were described already in the 19th century (e.g. Reinke & Berthold, 1879).

Appel & Wollenweber (1910, 1913) set new standards in describing pure-cultures that led to monographs of *Cylindrocarpon* (Wollenweber, 1929) and *Fusarium* (Wollenweber & Reinking, 1935). Using anamorphs grown from ascospores, Wollenweber (1924, 1926) produced a first general synopsis of holomorphs in the *Hypocreales*. Possibly because Wollenweber mainly worked on plant pathogens, only few taxa of the *Bionectriaceae* and none of *Bionectria* were treated.

Petch (1938), in a review of British *Hypocreales*, emphasized the importance of teleomorph–anamorph connections for future studies.

Dingley (1951) noticed the absence of distinctive teleomorphic characters to be used in generic separations and found that some critical characters were ephemeral so that herbarium specimens might not be reliable. Dingley (1957) introduced life cycle studies and illustrated anamorphs grown in culture from ascospores. Several informal sections were distinguished in *Nectria* based on only a few characters of the teleomorphs but characterized by common patterns in the anamorph. Some species of *Bionectria* were placed in *Nectria* group I, which was characterized by sporodochial anamorphs and partly by verticillium-like conidiophores. Dingley was thus the first to emphasize the holomorph of *Bionectria*. In the same year, Smalley & Hansen (1957) reported the connection of *Clonostachys rosea* (cited as *G. roseum* (Link) Bainier) to *B. ochroleuca* in culture (which they newly described as *N. gliocladioides*). The connection was confirmed by isolates from single ascospores obtained from perithecia grown in culture.

Booth (1959) distinguished nine groups of *Nectria*-like species based on holomorphic characters. He basically built up groups centred on species originally recognized by Fries, viz. *N. cinnabarina*, *N. coccinea* (Pers. : Fr.) Fr., *N. aquifolii* (Fr.) Berk., *N. episphaeria* (Tode : Fr.) Fr., and *N. peziza* (Tode : Fr.) Fr. With the exception of *N. aquifolii* and *N. coccinea*, these groups still form the basis of some of the recently recognized genera: *Nectria s.s.* (anamorphs *Tubercularia*), *Cosmospora* Rabenh. (anamorphs partly fusarium-like), and *Hydropisphaera* (anamorphs acremonium-like) (Rossman *et al*., 1999). To these he added groups based on *N. ochroleuca* (Schw.) Berk. (= *Bionectria*, anamorphs gliocladium-like), *N. arenula* (Berk. & Broome) Rossman & Samuels (*Hydropisphaera*, ana-

morph acremonium-like), *N. mammoidea* Phil. & Plowr. (anamorphs *Cylindrocarpon*), and the genus *Lasionectria* (Sacc.) Cooke (anamorphs acremonium-like). Booth (1959) underestimated the importance of differences in ascocarp pigmentation in *Nectria s.l.* and included *B. ralfsii* (ascocarps KOH–) in the *N. cinnabarina*-group (*Nectria s.s.*; ascocarps KOH+). Because Booth restricted his revision to British collections, the groups distinguished contained only few species.

Samuels (1976a) reviewed the species of Saccardo's subgenus *Hyphonectria* based on the type specimens and holomorphic characters derived from fresh material. The species were transferred to four unrelated genera, *Ciliomyces* Höhn. (= *Paranectria* Sacc., *Bionectriaceae*), *Herpotrichia* Fuckel [*Dothideales*, linked to coelomycetous anamorphs (Barr, 1984)], *Hypomyces* (Fr.) Tul. (today *Hypocreaceae*), and eight informal '*Nectria*'-groups. Samuels accepted some groups established by Booth, but rearranged several species, for example based on the KOH colour reaction of the ascocarps, and added new groups based on *N. candicans* (Plowr.) Maire (now *Nectriopsis* Maire, anamorphs generally acremonium-like), *N. subfalcata* Hennings (now *Protocreopsis* Doi, partly overlapping with Booth's *Lasionectria*, anamorphs acremonium-like), *N. haematococca* Berk. & Broome (now *Haematonectria* Samuels & Nirenberg, anamorphs fusarium-like), *N. leucorrhodina* (now *Dimerosporiella* Speg., anamorphs acremonium-like where known), and *N. muscivora* (not yet raised to generic level). Samuels (1976b, 1978) characterized holomorphic species according to their acremonium-like conidiophores that today are placed in various genera; they either form 1-celled conidia (1976b) or pluriseptate conidia (1978). Today most of these species groups are recognized at generic level. For several of these genera, like *Bionectria*, names were retrieved from formerly described but not widely accepted hypocrealean genera (Rossman *et al*., 1999).

Rossman (1983) treated *Nectria*-like taxa with multiseptate ascospores that were classified in existing groups delimited by Booth or Samuels or in the genera *Ophionectria* Sacc. (anamorph *Antipodium* Piroz.), *Calonectria* Sacc. (anamorphs *Cylindrocladium* Morgan, *Paranectria* Ces. & De Not. (anamorph unknown), or *Trichonectria* Kirschst. (anamorph acremonium-like where known). Rossman based her taxonomy mainly on teleomorphs or on holomorphs as far as connections of teleomorphs and anamorphs were known. *Nectria spirostriata* Rossman, characterized by striate, multiseptate ascospores and by synnemata forming greenish black conidial masses, for example, was placed in the *N. ralfsii*-group because of the pigmentation of the conidial masses. Two species of this group with 1-septate ascospores (*N. ralfsii* and *N. pityrodes*) are here accepted in *Bionectria*, while *Nectria spirostriata* was transferred to *Peethambara* Subram. & D.J. Bhat (Rossman *et al*., 1999).

CLASSIFICATION OF ANAMORPHS

Hyphomycete-generic concepts of early authors (e.g. Corda, 1839) were based on clear phenotypical discontinuities of structures examined on the natural substratum. The concepts of these genera were frequently narrow, not necessarily considering infrageneric variations and genus-overlapping character patterns because only few species were initially included. With time, however, a complex system was developed, within which taxonomic categories were proposed, for example according to the presence and absence and the kind of conidiomata produced, characters of the conidia such as septation and shape, and the pigmentation of the conidial masses. This sporological system resulted in artificial classifications of most of the taxa, because (i) it overemphasized single and particularly simple, thus likely polyphyletic, characters and (ii) it was developed independently from the classification of the teleomorphs, which were classified in similar schemes. However, the deuteromycete system was always seen as artificial (De Bary, 1854; Tulasne & Tulasne, 1861; Fuckel, 1870). While the dual system of classification resulted from the teleomorph–anamorph pleomorphism, a strictly anatomical system that regards genera as monomorphic, could result from the parallel classification of synanamorphs in different genera (Hennebert, 1971).

Hughes (1953) grouped hyphomycetes according to types of conidiophores and conidium development, treating characters of the conidia as secondary. This ontogenetic approach can be seen to a certain extent as analogous to the ontogenetic approach introduced by Luttrell (1951) for the teleomorphs. Later it was found that different modes of, or at least considerable variations in, conidial development can occur in closely related ascomycete taxa (Minter *et al*., 1982; Glawe, 1989, for species of the *Diatrypaceae*; Rogerson & Samuels, 1993, for species in *Hypomyces*; Seifert *et al*., 1997, for *Spicellum roseum* and *Trichothecium roseum*).

Connections between teleomorphs and anamorphs of species now classified in *Bionectria* were described by Reinke & Berthold (1879), Juel (1925), Dingley (1957), Smalley & Hansen (1957), Booth (1959), Samuels (1976a), and Samuels *et al*., 1990), of which the anamorphs were described in the genera *Clonostachys*, *Dendrodochium*, *Gliocladium*, *Myrothecium* sp., or *Verticillium*. In addition to these, anamorphs described independently from their *Bionectria* teleomorph were classified in *Acrostalagmus*, *Clonostachyopsis*, *Gliocladochium* Höhn. *Sesquicillium*, *Penicillium* Link, *Spicaria*, ?*Tubercularia* Tode, and *Verticilliodochium* Bubák.

While the plurality of anamorph genera linked to *Bionectria* may suggest that anamorphs are of less significance for the delimitation of naturally related species groups, the opposite view is taken in this monograph (see 'Generic concept').

Table 1. Terminology of conidiophores of *Bionectria* / *Clonostachys*.

Conidiophore terminology	Description	Representative taxa	Illustrations
Primary conidiophores	Mononematous, early formed; sparsely branched; branches and phialides divergent or adpressed; mono- to terverticillate or more-level verticillate; stipes long in relation to the penicilli; phialides relatively long; intercalary phialides absent; conidia held in watery heads; mostly associated with secondary conidiophores		
1. acremonium-like	Solitary phialides formed on 1 or 2 supporting cells	rare, few species of subgen. *Zebrinella*	Fig. 72 d Fig. 74 a
2. verticillium-like	Phialides and side branches ± divergent, in terminal whorls, more-level verticillate, or solitary from lower levels	subgen. *Bionectria*: *C. rosea*-complex	Fig. 16 a Fig. 23 a Fig. 33 c
3. gliocladium-like	Phialides and branches ± adpressed, mono- to terverticillate	subgen. *Bionectria*: *C. solani*-complex; subgen. *Zebrinella*	Fig. 36 b Fig. 41 c Fig. 63 a
Secondary conidiophores	Mononematous or synnematous, sporodochial; mostly frequently branched; bi- to quaterverticillate, more-level verticillate; side branches and phialides divergent and/or adpressed; stipes relatively short or of same height as the penicillus; phialides relatively short; intercalary phialides absent to abundant; conidia imbricate, held in chains or columns that can collapse to slimy masses; mostly associated with primary conidiophores, sometimes monomorphic		
1. clonostachys-like	Phialides in terminal or subterminal whorls; intercalary phialides rare or absent		
– adpressed	Penicilli adpressed, mostly forming single, long, narrow conidial columns	subgenera *Bionectria* (*C. rosea*-complex) also in other groups or subgenera	Fig. 16 b Fig. 43 d
– divergent	Penicilli divergent; phialides somewhat divergent or adpressed, forming broad, frequently short conidial chains that may collapse early to a slimy mass	subgenera *Bionectria* (*C. solani*-complex), *Zebrinella*, rare in *Epiphloea*	Fig. 36 d, e Fig. 38 b
– with multiple conidial columns	Main branches ± divergent, each forming ± isolated units of ± adpressed penicilli	subgen. *Bionectria*	Fig. 32 a, b
2. dendrodochium-like	Conidiophores distinctly sporodochial; conidial masses whitish or pale- to light orange	subgen. *Bionectria*	Fig. 36 a Fig. 25 e
3. myrothecium-like	Conidiophores distinctly sporodochial; conidial masses pale- to dark green, sometimes almost black	subgenera *Myronectria*, *Astromata*, rarely in *Bionectria*	Fig. 51 a, b Fig. 57 g–l Fig. 60 c–f
4. small sporodochial	Conidial masses green; phialides on short metulae scattered densely along swollen hyphae or directly seated on angular to globose cells	subgen. *Astromata*	Fig. 56 j Fig. 57 a–c
5. sesquicillium-like	Intercalary phialides abundantly formed in the apical parts of the conidiophore, generally bearing a solitary terminal phialide; conidiophores sometimes setose	subgen. *Epiphloea*, *Uniparietina*, less frequent in subgen. *Zebrinella*, rare in subgen. *Bionectria*	Fig. 77 c Fig. 93 a, b Fig. 97 c

The use of anamorphs for recognizing natural relatedness, however, necessitates reinterpretations of certain characters, emphasis on character patterns, the consideration of transition series of particular character states, and considerations of their appearance on the natural substratum as well as in pure culture.

Clonostachys.— Corda (1839) described *Clonostachys* with the only species *C. araucaria*, characterized by penicillate conidiophores and imbricate conidia held in columns. Corda indicated only one kind of conidiophore. Probably the first species to be classified in *Clonostachys* was described by Link (1816) as *Penicillium roseum*. It was neotypified with a strain formerly identified as *Gliocladium roseum* Bainier and transferred to *Clonostachys* as *C. rosea* (Link) (Schroers *et al*., 1999b). While the genus *Gliocladium* Corda gained acceptance for anamorphs forming penicillate conidiophores with slimy conidial masses, *Clonostachys* was rarely used, for example for *C. araucaria* var. *rosea* Preuss (1852) and *C. populi* Harz (1871), or it was widely considered as a synonym of

Gliocladium. Bainier (1907b) described a new species, *Gliocladium roseum*, emphasizing the formation of two kinds of conidiophores. Because Bainier (1905) described another such species in *Acrostalagmus*, *A. roseus* (1905; interpreted here as a synonym of *Clonostachys solani*), he obviously did not recognize conidiophore dimorphism as generically relevant. Thom (1910) described the same character patterns but referred to *Penicillium roseum* Link (1816) as the likely basionym. The citation *G. roseum* (Link) Bainier is, however, illegitimate because Bainier described a new species and did not refer to Link. Pinkerton (1936) recognized the genus *Clonostachys* and described an additional variety, *Clonostachys araucaria* var. *confusa* Pinkerton, for Bainier's *G. roseum* and mentioned Link's *P. roseum* as a possible synonym. The synonyms of *G. roseum* listed by Isaac (1954) and Domsch *et al*. (1980) are here partly reviewed. The taxa described by Preuss, Harz, and Pinkerton are considered as synonyms of *C. rosea* based on their original descriptions and drawings (reviewed in Schroers *et al*., 1999b). Hawksworth and Gams (in Hawksworth & Punithalingam, 1975) transferred *Verticillium compactiusculum* Sacc. to *Clonostachys* because of the penicillate conidiophores and the conidial columns and discussed its differences from *C. rosea*. Domsch *et al*. (1980) and Gams (1984) summarized the discussions for the possible generic distinction of the genera *Gliocladium* and *Clonostachys* by emphasizing the differences in the teleomorphs. Gams (1984) also introduced the descriptive terms 'primary conidiophores' for the verticillium-like- and 'secondary conidiophores' for the penicillate conidiophores, pointing to a chronological sequence in their appearance and a tendency of the latter to form sporodochia (Table 1). Samuels (1988b) identified the anamorphs of several holomorphic species as *Clonostachys* sp. In doing so, he indicated their relatedness to species of the *Nectria ochroleuca*-group. These anamorphs, however, were partly characterized by monomorphic, gliocladium-like conidiophores forming conidial masses in slimy heads (Table 1).

Spicaria.— The genus *Spicaria* was introduced by Harting (1846) for *S. solani* observed on potato. The conidiophores illustrated are similar to primary, narrowly adpressed conidiophores of species here placed in the *Clonostachys solani* complex. Harting did not describe solitarily formed secondary conidiophores but illustrated a sporodochium that probably contained such conidiophores. This sporodochium is more or less indistinguishable from that observed in *Clonostachys solani* (Fig. 36 a). Therefore *S. solani* is neotypified here with the anamorph of a *C. solani* specimen. The synonymy of *Clonostachys* and *Spicaria* is based on the dimorphic conidiophores illustrated by Harting and the similarities of the sporodochia, at least when observed on the natural substratum. This identity of *S. solani* was already suggested by Petch (1944) who made the combination *Gliocladium solani* (Harting) Petch, taken up by Domsch *et al*. (1980). Harz (1871) newly described *Spicaria nivea* as a fungus forming verticillately branched conidiophores and long chains of conidia that are connected in an end-to-end fashion. This character pattern is considered typical of *Paecilomyces* (Brown & Smith, 1957). Other authors, including Saccardo (1886, 1906), followed the misinterpretation introduced by Harz, ignoring Harting's original description and included species in *Spicaria* that are now classified in *Paecilomyces*, *Mariannaea* (see Brown and Smith, 1957; Samson, 1974), and other genera. The confusion around *Spicaria* culminated in the description of the homonymous *Spicaria solani* Rivolta 1873. Hughes (1951) and Brown and Smith (1957) finally considered *Spicaria* a *nomen confusum*. Sporodochia with pale, non-greenish conidial masses as were described by Harting for *S. solani* are called dendrodochium-like in this revision (Table 1).

Dendrodochium.— The genus *Dendrodochium* was described by Bonorden (1851) as having sporodochia that break through wood, with divergently branched conidiophores. The genus *Dendrodochium* thus has become a depository for sporodochial and myrothecium-like species. No type material is left from Bonorden's fungi but the sporodochia described by Bonorden are similar to those found in many species of *Bionectria* and to the sporodochium illustrated by Harting (1846). In this paper, *Dendrodochium* is interpreted as a synonym of *Clonostachys*. The neotypification of the type species, *D. aurantiacum*, establishes its synonymy with *Spicaria solani* Harting. To describe robust sporodochia forming white to pale orange, non-greenish conidial masses, the term dendrodochium-like is used in this revision (Table 1).

Clonostachyopsis.— Von Höhnel (1907) compared his genus *Clonostachyopsis* with *Clonostachys* and described conidia that are arranged in imbricate chains, but, in contrast to *Clonostachys*, originate laterally from hyphae. Although such intercalary phialides are common in *Clonostachys* and *Sesquicillium*, it is possible that Von Höhnel incorrectly interpreted these structures and possibly saw overmature conidiophores with intact conidial columns but without phialides. Therefore *Clonostachyopsis* was synonymized with *Clonostachys* (Schroers *et al*., 1999b).

Verticilliodochium.— The genus *Verticilliodochium* was described by Bubák (1914) for a sporodochial fungus that he identified as *Verticillium tuberculariodes* Speg. formed on a stroma erumpent through bark, enclosing a subcortical ascomycete (his Fig. 1, Tab. 8). This habit is typical, particularly for the perithecial stroma in subgenus *Bionectria*. Bubák also illustrated slightly curved conidia showing a laterally displaced hilum and subcortically growing mycelium

that formed an erumpent, pseudoparenchymatous stroma from which the sporodochia developed. Based on the description and illustrations provided by Bubák, there is no doubt that he had the anamorph of a *Bionectria* species. The synonymy of *Verticilliodochium* and *Clonostachys* was established elsewhere (Schroers *et al*., 1999b).

Gliocladochium.— The genus *Gliocladochium* Höhn. (1926) was described for *Periola tomentosa* Fr. Von Höhnel described sporodochia consisting of penicillate conidiophores forming slimy pale to black masses of hyaline conidia, measuring 5–6 × 2.5–3.5 µm. Similar characters, but with only white structures, were illustrated for this fungus by Kirchner & Boltshauser (1898). The dark conidial masses mentioned by von Höhnel may refer to myrothecium-like anamorphs of *Clonostachys*. No such dark structures, however, are mentioned by Fries (1822) for the type species of *Periola*, *P. tomentosa.* Because von Höhnel did not refer to the original material of Fries [but to a specimen of Fuckel (Fuckel, 1870: 369, Fungi rhen. no. 203) and Desmazières (Plantes cryptogames de France, 1843, no. 1318)] and because no original material of Fries is available in UPS, the identity of *Periola tomentosa* is considered doubtful. Massee (1893) under this name illustrated acremonium-like conidiophores forming chains of obovate conidia belonging to a different species.

Sesquicillium.— Gams (1968) introduced the genus *Sesquicillium* for species that form conidia both from terminal cells of penicillate conidiophores [telophialides in the terminology of Gams (1971)] and intercalary phialides with short lateral conidiogenous necks [similar to pleurophialides in the terminology of Von Arx & Gams (1967) and Gams (1971)]. In *Sesquicillium*, mostly one intercalary phialide is associated with one terminal phialide. Gams therefore chose the Latin *sesqui* (one and a half) to derive the generic name. Rarely, two intercalary phialides arise below one terminal phialide. Phialides in *Sesquicillium* typically form imbricate chains of conidia and the aggregation of several such chains leads to complex columns. Based on these characters, *Sesquicillium* was regarded as similar to *C. rosea* (Gams, 1968). Two species, *Fusidium buxi* Schmidt : Fr. and *Verticillium candelabrum* Bonorden, were originally combined in *Sesquicillium* by Gams (1968).

For good morphological reasons, a relatedness between *Sesquicillium* and *Clonostachys* has been assumed by Gams (1968) and Samuels (1989): (i) both genera form penicillate conidiophores (with the secondary conidiophore in *Clonostachys* possibly being homologous to the conidiophores formed in *Sesquicillium*); (ii) at least one species of *Sesquicillium*, *B. sesquicillii*, also forms a verticillium-like synanamorph, comparable to the primary conidiophores in *Clonostachys*; (iii) most species of both genera form conidia with a laterally displaced hilum; (iv) in both genera the conidia are held in imbricate chains and complex columns; (v) even in other species of *Clonostachys* intercalary phialides can be found at least rarely and particularly in species of subgenus *Zebrinella*; (vi) Turhan (1993) reported a destructive mycoparasitism for an unidentified strain of *Sesquicillium* similar to that described for *C. rosea* (Barnett & Lilly, 1962; and subsequent papers). Based on these similarities, *Sesquicillium* is considered a synonym of *Clonostachys* here. For conidiophores that contain abundant intercalary phialides the term sesquicillium-like is used (Table 1).

Vittal (1974) described *Sesquicillium setosum*, which was distinguished by relatively long cylindrical phialides and setae originating mainly from the base of the conidiophores. Although no type material could be obtained, *S. setosum* has been accepted and some isolates corresponding to the description are available. Because of a similar habit of setae and conidiophores, *S. setosum* was suspected to have an affinity with *Cylindrocladium* (Bissett, 1983). Intercalary phialides, however, are unknown in *Cylindrocladium*. The species is here neotypified by an ascospore isolate of the newly described teleomorph, *Bionectria setosa*.

Another species with intercalary phialides is *Sesquicillium microsporum* (Jaap) W. Gams & Veenbaas-Rijks (Veenbaas-Rijks, 1970; Gams, 1971). It differs from other *Sesquicillium* species in size ranges of phialides and conidia (Samuels, 1989: Figs 7–9) and a partly myxomyceticolous life-style (Rogerson & Stephenson, 1985). Bissett (1983) transferred *S. microsporum* to *Tolypocladium* W. Gams because of the rather irregular branching pattern in the conidiophores, false phialidic whorls, elongated phialidic necks, and slimy masses of conidia. Phylogenetic inferences from the LSU rDNA place *S. microsporum* in a supported clade together with two myxomyceticolous species of *Nectriopsis* (not shown). Within the *Bionectriaceae*, *S. microsporum* is thus closely related to but not congeneric with the sesquicillium-like anamorphs that are classified in *Bionectria*/*Clonostachys*.

Myrothecium.— The type species of *Myrothecium* is *M. inundatum* Tode : Fr, which is characterized by penicillate conidiophores, sporodochial conidiomata, green to dark green conidial masses, and marginal hyphae and/or thick-walled, erect setae that extend somewhat beyond the hymenium. Sporodochia of *Myrothecium* therefore are described as cupulate (Tulloch, 1972). Tode included 5 species in *Myrothecium*, of which Fries accepted three, *M. inundatum*, *M. roridum* Tode : Fr., and *M. verrucaria* (Alb. & Schw. : Fr.) Ditm. that were neotypified by Tulloch (1972). Tulloch (1972) expanded the concept of *Myrothecium* to include synnema-like anamorphs such as *M. masonii* Tulloch, *M. atrum* (Desm.) Tulloch, and *M. prestonii* Tulloch. Her concept was considered as too broad

(Nag Raj, 1995), particularly because of the emphasis on the conidial colour over the morphology of the conidiophores and conidiomata.

Molecular data indicate relatedness of *M. inundatum*, *Peethambara*, and *Albosynnema* (all forming green-coloured conidial masses) to the *Hypocreales* (Rossman *et al*., 1999) however, do not support their classification in the *Bionectriaceae* as was suggested earlier (Rossman *et al*., 1999). Since the *Bionectria*-clade contains several species forming sporodochia and green conidial masses, Nag Raj's criticism of Tulloch's emphasis on conidial colour appears justified.

While only little can be said about the natural relatedness of the diverse anamorphs treated by Tulloch (1972), the myrothecium-like anamorphs in *Bionectria* are best characterized by imbricate conidial chains that sooner or later collapse to slimy or watery-slimy masses, ovoidal or slightly curved conidia mostly having laterally displaced hila, absence of conidial appendages, absence of sporodochial setae both on the natural substratum and in culture, and absence of warted or curled sterile elements. A deviant species in *Bionectria* is *B. pityrodes* (subgenus *Bionectria*) because of its differentiated sporodochial margin.

The principal characters used to delimit *Myrothecium* as described by Tulloch (1972) were derived from studies of specimens from the natural substratum. The setae characteristic of some of the *Myrothecium* species, however, may be lacking in culture (K.A. Seifert, pers. comm.). Thus, the lack of sporodochial setae is not necessarily indicative of *Bionectria*.

Sporodochia forming green pigmented conidial masses are here called myrothecium-like (Table 1).

Gliocladium.— The genus was described by Corda (1840) with the only species *Gliocladium penicillioides*, of which no type material remains. The interpretation of Corda's description and illustration is unequivocal because of the substratum mentioned (basidiomes of '*Thelephora*' *hirsuta* and *T. sanguinolenta*, both now in *Stereum* Pers.). The genus has become a repository of heterogeneous penicillate anamorphs with stalked slimy spore drops, including some anamorphs with dimorphic conidiophores and imbricate conidial chains (*Clonostachys s.s*.). *Gliocladium* was considered to be the slimy counterpart of *Penicillium* Link (Thom, 1910, 1930). In its strict sense, the genus comprises anamorphs of *Sphaerostilbella* and *Hypocrea* series *Pallidae* Doi (*Hypocreaceae*), which mainly occur on aphyllophoralean basidiomes (Samuels, 1976a; Seifert, 1985; Schroers *et al*., 1999b). The conidiophores of these species are characterized by long, frequently wide, warted or smooth stipes, short adpressed penicilli, phialides in pluriverticillate terminal whorls, and watery to slimy, round heads of conidia. Several species of *Sphaerostilbella* form synnemata (Seifert, 1985). The polyphyletic distribution of gliocladium-like taxa has been demonstrated by analyses of LSU rDNA sequences (Rehner & Samuels, 1994). Anamorphs of holomorphic species that are unrelated to *Gliocladium s.s*. are either referred to as gliocladium-like or are placed in different genera, if other phenotypic characters clearly allow segregation from *Gliocladium* (as it was proposed for *Clonostachys* and *Rhopalocladium* in Schroers *et al*., 1999b). However, the conidiophores of several species of *Clonostachys* are gliocladium-like (Table 1), being narrowly penicillate and forming watery to slimy conidial heads. The primary conidiophores of species of the *Clonostachys solani* complex and members of the subgenus *Zebrinella* resemble the conidiophores of *Gliocladium s.s*.

Verticillium and **Acrostalagmus**.— *Verticillium* Nees 1816 comprises anamorphs with divergent branches and whorls of divergent phialides. Gams (1971) and Gams & van Zaayen (1982) distinguished several sections in *Verticillium*, of which section *Verticillium* contained a single species, *V. luteo-album* (Link : Fr.) Subram., of which *V. tenerum* Nees : Fr. (the type species of *Verticillium*) and *Acrostalagmus cinnabarinus* (the type species of *Acrostalagmus* Corda) are later synonyms (Hughes, 1951, 1958; reviewed in Domsch *et al*., 1980).

The morphological similarity of *Verticillium* and *Clonostachys* is mainly related to the verticillium-like synanamorphs formed by numerous species of *Clonostachys* that, however, are less highly branched, never form brownish orange conidial masses, and typically are accompanied by secondary, penicillate conidiophores. The conidiophore dimorphism of *Clonostachys* was first explicitly described and illustrated for *Acrostalagmus roseus* by Bainier (1905), a species identical in all characters to *Clonostachys solani*. Another species, *Verticillium intertextum* Isaac & Davis (Isaac & Davies, 1955), is considered as a synonym of *C. rosea*, although it only forms primary conidiophores. Divergently branched primary conidiophores are called verticillium-like in this revision (Table 1).

Tubercularia.— The genus *Tubercularia* Tode 1790 was reviewed by Seifert (1985) and Rossman (1989). *Tubercularia* is restricted to the anamorphs of *Nectria s.s.* and related anamorphic species. Its conidiomata can be sporodochial, synnematous or pycnidial; they differ from the sporodochia formed in *Clonostachys* by a positive colour reaction in KOH, frequent occurrence of chains of intercalary phialides, particularly at the margin of the conidiomata, conidia held in dense slimy masses (never in imbricate chains), and in more deeply pigmented, orange, pink, brownish, or with age blackish conidial masses. While species of *Clonostachys* also form well-developed anamorphs in culture, those of *Tubercularia* frequently are poorly developed.

Volutella.— A synopsis of some species of *Volutella* Fr. 1832 is given in Domsch *et al*. (1980). Species of *Volutella* are phenotypically similar to those of *Myrothecium*, particularly because of the setae formed throughout the sporodochium, but they differ in having pale-coloured, non-greenish conidial masses. The genus has never been monographed. Until now, species of *Volutella* have been linked to *Pseudonectria* Seaver and *Cosmospora* (Samuels, 1977), which are genera of the *Nectriaceae*. Phenotypically related to *Volutella* is *Sarcopodium* Ehrenb. 1818, which is characterized by warted, partly undulate, and brightly pigmented setae (Sutton, 1981). *Kutilakesa* Subram., which was considered as a synonym of *Sarcopodium* by Sutton (1981) has been linked to a species of *Nectriella* Nitschke ex Fuckel, including *N. pironii* Alfieri & Samuels (Alfieri & Samuels, 1979).

Penicillium.— The genus *Penicillium* comprises anamorphs of the *Trichocomaceae*, *Eurotiales*. The penicillate conidiophores are characterized by smooth or warted stipes, ± adpressed penicilli, phialides in terminal whorls, and hydrophobic conidia in dry, connected chains. The genus, described by Link (1809), is neotypified with a strain of *P. expansum* (Samson *et al*., 1976). Link (1816) described *P. roseum*, of which the original material is lost, as a fungus from potato forming pinkish conidial masses that are unusual for *Penicillium* but typical of *Clonostachys*. *Penicillium roseum* was neotypified with a strain formerly identified as *Gliocladium roseum* Bainier and transferred to *Clonostachys* (Schroers *et al*., 1999b).

Paecilomyces.— The genus *Paecilomyces* Bain. (Bainier, 1907a) comprises species with penicillate conidiophores forming conidia held in unpigmented, dry chains. The form-genus is characterized by flask-shaped phialides consisting of a wide, frequently cylindrical venter that abruptly tapers into a long, also cylindrical neck. The type species of *Paecilomyces* is morphologically and phylogenetically related to *Penicillium*. The phialides resemble those of *Mariannaea* spp., which are disposed in verticillate whorls. In contrast to *Mariannaea* and *Clonostachys*, the conidia in *Paecilomyces* are arranged in linear chains being connected end-to-end. In the treatments of the genus by Onions & Barron (1967) and Samson (1974), several species with clavicipitalean affinity are included. The genus is still heterogeneous and requires further revisions. Samson (1974) distinguished two sections in *Paecilomyces* according to colony pigmentation and the general formation of cleistothecia in culture that belong to *Byssochlamys* Westling, *Talaromyces*, or *Thermoascus* Miehe. For the confusion of *Paecilomyces* with *Spicaria* Harz see notes on *Spicaria* Harting above. Brown and Smith (1957) listed many authors who used *Spicaria* Harz for *Paecilomyces*-like fungi. *Paecilomyces* is easily distinguishable from *Clonostachys* because of the dry linear conidial chains, shape of the phialides, and mostly dark brown, yellow-brown, or violet colony pigmentations.

Mariannaea.— The genus *Mariannaea* G. Arnaud was invalidly proposed (Art. 36.1, ICBN) by Arnaud (1952) based on *Penicillium elegans* Corda and validated by Samson (1974). It comprises anamorphs with verticillium-like conidiophores, flask-shaped phialides that ± abruptly taper into an almost cylindrical neck (similar to those in *Paecilomyces*) (Arnaud, 1952: Fig. 2A), and brownish to red purple colonies (Samson, 1974). Species of *Mariannaea* are particularly characterized by long, non-columnar chains of imbricate conidia that arise from each of the divergent phialides (Arnaud, 1952: Fig. 2A). Conidiophores in *Mariannaea* are monomorphic, however, in one species a verticillium-like type of conidiophores is associated with more highly branched, penicillate conidiophores, on which the conidial chains early collapse into botryose masses (unpubl.). While the dimorphic conidiophores may suggest a close relationship to *Clonostachys*, the brown colony pigmentation resembles that formed for example by *Cylindrocladium* (*Nectriaceae*). The single known teleomorph of *Mariannaea*, '*Nectria*' *mariannaeae* Samuels & Seifert, consists of yellowish to brownish perithecia (Samuels & Seifert, 1991), thus resembling those of the *Bionectriaceae*. However, while Samuels and Seifert (1991) described the ascomata as KOH–, a weak positive KOH reaction of the ostiolar region of the perithecia was observed (Schroers, unpubl.). This weakly positive KOH reaction indicates a relationship of *Mariannaea* to the *Nectriaceae*, which is supported by sequences of the partial LSU rDNA (Schroers, unpubl.).

Rhopalocladium.— The unispecific genus *Rhopalocladium* Schroers, Samuels, & W. Gams was described for the anamorph of *Nectriopsis sporangiicola* (Samuels) Samuels, *R. myxophilum* (Schroers *et al*., 1999b). Conidiophores in *Rhopalocladium* are gliocladium-like, however, have several characters that clearly distinguish them from conidiophores formed in *Gliocladium s.s.* and other taxa with gliocladium-like anamorphs [compare Schroers *et al*., 1999b: Figs 36–38, 42, 43 with Figs 34, 35, 39, 40 (for *Gliocladium penicillioides*) and 45, 46 (for *Roumegueriella rufula* (Berk. & Broome) Malloch & Cain)]. These characters include very long and up to 15 µm wide conidiophore stipes, cells of the penicillus that are narrowly attached to their supporting cells and widening upwards (clavate), and, compared to the clavate metulae, very narrow, ± subulate phialides that form conidia in white, watery to slimy, globose masses. Based on sequence analyses of the partial LSU rDNA (Rossman *et al*., 2001), *Rhopalocladium myxophilum* forms a well-supported clade together with *Nectriopsis violacea* (Fr.) Fr. (anamorph acremonium-like), the type species

of the genus *Nectriopsis*, and *Sesquicillium microsporum* (not shown). All these species are characterized at least partly by a myxomyceticolous life-style (Rogerson & Stephenson, 1985; Samuels, 1973) but have conspicuously diverse anamorphs.

Nectriopsis was established by Maire (1911) for a few species formerly classified in *Hypomyces*. Weese (1913) lectotypified *Nectriopsis* Maire with *N. violacea* (Fr.) Fr., a myxomyceticolous species. Today the genus is recognized in the *Bionectriaceae* (Rossman *et al*., 1999) after its name was proposed for conservation against the hardly known genera *Chrysogluten* Briosi & Farneti and *Dasyphthora* Clem. (Rossman & Samuels, 1998). Several of the species treated by Samuels (1988a) were moved to *Dimerosporiella* Speg. (Rossman *et al*., 1999). However, *Nectriopsis* is still broadly delimited, comprising myxomyceticolous, fungicolous, lichenicolous and herbicolous fungi that are characterized by a perithecial wall consisting of a single region (Samuels, 1988a). Phylogenetic inferences based on sequences of the ITS and/or LSU rDNA (Rossman *et al*., 2001) indicate that *Nectriopsis s.s*. could be restricted to myxomyceticolous species such as *N. violacea*, *N. sporangiicola*, and those treated by Samuels (1973).

MATERIAL AND METHODS

Field work.— Fresh material was collected mainly in the U.S.A. (North Carolina and Puerto Rico), Japan, Australia (NSW), and New Zealand, and various countries of Europe. Twigs and branches of recently dead trees were scrutinized. Representative perithecia were removed and kept air-dried separate from the main collection for subsequent isolations. The main part of the specimens was dried with hot air.

Isolation.— Ascospores were taken from a single, fresh or air-dried perithecium directly or after placing the specimen in a moist chamber. The perithecium was placed in a drop of sterile tap water on a clean microscope slide and broken so that asci and ascospores were released. The drop of water was examined microscopically (without a cover slip) to check the state of maturity of the perithecium. The ascospores and asci were removed with a glass capillary and spread out on agar on a marked place near the edge of a Petri dish. Translucent CMA (Difco) or PCA (CBS) containing antibiotics to suppress bacterial growth was used. The remnant of the water drop was covered with a cover slip for observation of the ascospores. The Petri dish was kept at room temperature and checked for germinated ascospores after 7–12 hours. Ascospores with a short germ-tube were transferred to marked and clean areas of the same Petri dish by micromanipulation under the 10× objective of a microscope. The manipulation was performed with fine glass needles or glass forks using the techniques described by Skerman (1968) and Samuels (1979). Alternatively, masses of ascospores or whole asci were used for isolation. Agar blocks with isolated ascospores were moved to clean Petri dishes and incubated at room temperature or at 21°C. Subcultures of homogeneous colonies were transferred to agar slants. The original plate was dried and kept together with the herbarium specimen. Conidial isolates were obtained after keeping the specimen in a moist chamber. Newly developed slimy masses of conidia produced on sporodochia or on the tips of solitary conidiophores or phialides were touched with the tip of a sterile glass needle and streaked out on a Petri dish.

Herbarium specimens and morphological examination of the teleomorph.— Herbarium specimens were obtained from B, BPI, FH, IMI, K, L, LPS, NY, PAD, PDD, PH, PRM, and STR (abbreviations according to Holmgren *et al*., 1990). Perithecia were described from the natural substratum for their habit, colour, surface, size, and shape. One or several perithecia were removed, rehydrated in water, broken or cut longitudinally and observed microscopically in water or after replacing the water with lactic acid. The colour reaction of pieces of parts of the perithecia was checked in 3% KOH, lactic acid, or 3% KOH followed by lactic acid. Cross sections of perithecia and the supporting tissues of stromata and/or host were prepared from rehydrated pieces of the specimens supported in Tissue-Tek O.C.T. 4583 at –20°C using a Damon IEC CTF microtome cryostat. The 12–20 µm thick sections were observed in lactic acid.

Examination of living cultures.— Stock cultures were kept on agar slants on oatmeal agar (OA) or potato-carrot agar (PCA). Macroscopic descriptions were made from corn meal-dextrose agar (CMD, Difco), potato-dextrose agar (PDA, Difco) and OA, microscopic descriptions from CMD or OA. For inoculation, conidial masses were streaked out and incubated either in darkness at 24°C or at room conditions (diffuse daylight, light/dark rhythm, 15–26°C), or under near UV light at 23–26°C. Growth rates and pigmentation were recorded and macroscopic characters were described after 7 d or more; colours of the colony reverse were determined according to Kornerup & Wanscher (1978). Micromorphological characters were recorded mostly from 6–12-d-old colonies using structures from relatively young parts of the colony; drawings were made in water or lactic acid (*ca* 90 %). For observing particular morphological features (ascospore ornamentation and ascus tips from the natural substratum) cot-

ton blue/lactic acid and phase contrast were used. Cardinal temperatures were determined at 12–36°C in steps of 3°C in darkness. The inoculum was an agar cylinder of *ca* 3 mm diam that was cut out from relatively young parts of CMA or OA colonies using a cork borer. Colony diameters were measured after 7 days at 24°C if not specified differently.

Microscopy, measurements and documentation.— Perithecia of representative collections were photographed under a Leitz dissecting microscope (DM). Microscopical observations were made using the light microscopes Zeiss Axioplan (LM, DIC, PC), Olympus BX 50 (LM, DIC), or Zeiss (LM, formerly used by Von Arx and Seifert). Microscopic measurements, drawings, photographs, and descriptions of morphological characters (surface, subsurface view of the perithecial wall, asci, ascospores, conidiophores, conidia, etc.) were made from microscopical preparations in water or lactic acid with the aid of image analysis or using a camera lucida. Drawings were made with a camera lucida, mostly using DIC.

Magnifications in drawings.— Reproductive structures (asci and conidiophores), non-discharged ascospores, and the perithecial seta in Fig. 98 c are drawn at 1:1000 magnification, unless otherwise indicated (Figs 7, 26 f, 90 b, 93 b). All free ascospores and conidia as well as the cells of the perithecial wall in Fig. 81 c are drawn at 1:2000, unless otherwise indicated (Fig. 7). Please note that some structures may be placed closely juxtaposed to the improper bar.

Terminology.— Morphological terms follow Hawksworth *et al*. (1995). Terminology for conidiophore branching is taken from Seifert (1985) and conidial shape is partly described as in Gams (1971). Other terms used are explained below. Terms for the descriptive statistics follow Sokal & Rohlf (1997).

Descriptive statistics.— Measurements in the description are given as (i) n_1–n_2; (ii) n_1–n_3–n_2, or, (iii) (n_1–)n_4–n_3–n_5(–n_2), with n_1 = minimum value observed; n_2 = maximum value observed; n_3 = arithmetical means; n_4/n_5 = first/third quartile. The values were calculated using the statistical software XLSTAT 4.0 (T. Fahmy, www.xlstat.com). Measurements of asci and cells of the perithecial wall were rounded to the nearest 0.5 µm, those of spores and phialides to the nearest 0.2 µm.

DNA extraction and amplification.— Strains used for the molecular studies are listed in Table 2. The mycelium for DNA extraction was grown and harvested as described elsewhere (Schroers, 2000). The DNA was extracted using a CTAB procedure adopted from Weising *et al*. (1995). In general the protocol of Gerrits van den Ende & de Hoog (1999) was followed but the extraction buffer contained 20 mM Na-EDTA, the chloroform extraction was followed by an extraction using 500 µl of chloroform-isoamyl alcohol (UCB, Belgium) (24:1), the DNA was washed twice with 500 µl ethanol (70 %, –20°C), and for resolving the DNA a TE-buffer was used containing 1 mM Na-EDTA.

The ITS-1, ITS-2, and the 5'-end of the LSU rDNA were amplified as described elsewhere (Schroers, 2000). The *tub*2 was amplified with the primers T1 and T22 (O'Donnell & Cigelnik, 1997) using the same reaction mix and procedures as for the rDNA. When amplification failed, 2 mM Mg-acetate (Merck A860219) were added to the PCR mix. The annealing temperature was between 55–60°C.

The sequencing reactions were done as described elsewhere (Schroers, 2000). For sequencing the partial *tub*2 the primers T1 (O'Donnell & Cigelnik, 1997) and CT41 (5'-GAA GTA GAC GTT CAT GCG CTC-3'; K. O'Donnell, pers. comm.) were used.

DNA data analysis.— The sequences were assembled and edited as described elsewhere (Schroers, 2000).

The coding regions of the *tub*2 (exons) were identified by comparison with those of published sequences of hypocrealean taxa (e.g. O'Donnell: U85583, *Fusarium* sp., NRRL 22192). To deduce the amino-acid sequences for all sequences, introns from the DNA sequences were eliminated in SeqmanII (DNAStar, Inc., Madison, Wisconsin). The exons were transformed to protein sequences in Megalign (DNAStar, Inc., Madison, Wisconsin). In some sequences the bases at the 5' end could not be identified with certainty. These data were coded as unknown. The DNA sequences of the partial β-tubulin gene and the predicted amino-acid sequences of its protein have been deposited in GenBank (AF358149–AF358224; Table 2).

Sequences of the rDNA (deposited in GenBank under the accession numbers AF210663–AF210670, AF210672–AF210691, and AF358225–AF358256; Table 2) were combined with the *tub*2 data using a text editor. Two data sets were prepared, with which several sets of analyses were carried out.

1. (Fig. 2): A data set consisting of sequences from the *tub*2 combined with the rDNA (ITS-1, 5.8S rDNA, ITS-2) comprised representatives of all subgenera in *Bionectria*. The introns of the *tub*2 were found to be diverse, although located on conserved places in the gene. The alignment used was entirely based on ClustalX (1.8;ftp://ftp-igbmc.u-strasbg.fr/pub/ClustalX) using multiple alignment parameters as follows: Gap opening 5; gap extension 3; DNA transition weight 0. The data were analysed by heuristic searches and optimized according to the maximum parsimony criterion.

2. (Fig. 3): Another data set identical to that described under 2 was confined to species of subgenus *Bionectria*, using *B. levigata* (subgenus *Zebrinella*) as outgroup. The sequence alignment was adjusted

Table 2. Taxa of *Bionectria* / *Clonostachys* and their origin, substratum, CBS strain number, as well as GenBank accession numbers of sequences used in the trees of Figs 2–5 or elsewhere (Schroers, 2000).

	Taxon name	Origin	Substratum	Strain (CBS)	Sequence accession number of	
					*tub*2	rDNA
02	*B. apocyni*	U.S.A, New York	dead stem of *Apocynum cannabinum*	130.87	AF358168	AF210688 [n]
03	*B. oblongispora*	Japan	bark of dying tree of *Orixa japonica*	100285	AF358169	AF358248 [m]
04	*B. kowhaii*	New Zealand	bark of ?*Sophora microphylla*	461.95	AF358170	AF358250 [m]
05	*B. ochroleuca*	Czech Republic	air in uranium mine	438.68	AF358163	
05	*B. ochroleuca*	Mexico	dead leaves of *Yucca* sp.	916.97	AF358164	
05	*B. ochroleuca*	U.S.A.	decaying bulb of *Lilium auratum*	194.57	AF358165	AF358237 [m]
05	*B. ochroleuca*	France	bark of *Salix* sp.	406.95	AF358167	AF358249 [m]
05	*B. ochroleuca*	Guyana	live rachis of *Pteridium aquilinum*	193.94	AF358159	AF210686 [n]
05	*C. rosea* f. *catenulata*	Ukraine	soil	126.72	AF358202	
05	*C. rosea* f. *catenulata*	U.S.A., Utah	soil	154.27	AF358160	AF358231 [m]
05	*C. rosea* f. *catenulata*	U.S.A., Wyoming	soil	443.65	AF358166	AF358233 [m]
05	*C. rosea* f. *catenulata*	Germany	soil	221.72b	AF358203	AF358234 [m]
05	*C. rosea* f. *rosea*	France	rotten cardboard	100502	AF358200	
05	*C. rosea* f. *rosea*	France	tuber of *Solanum tuberosum*	117.23	AF358201	
05	*C. rosea* f. *rosea*	U.S.A., New York	stored carrot roots	226.48	AF358198	
05	*C. rosea* f. *rosea*	U.S.A., New Jersey	soil	704.97	AF358197	
05	*C. rosea* f. *rosea*	U.S.A., Beltsville	isolated from *Ixodes* sp.	912.97	AF358199	
05	*C. rosea* f. *rosea*	Netherlands	soil, on sclerotia of *Sclerotinia minor*	710.86	AF358161	AF358235 [m]
05	*C. rosea* f. *rosea*	U.S.A., Massachusetts	on *Acer palmatum*	376.55	AF358162	AF358239 [m]
06	*B. byssicola*	New Zealand	on stem of *Persea americana*	101918	AF358150	
06	*B. byssicola*	U.S.A., Ohio	?	293.78	AF358152	
06	*B. byssicola*	Venezuela	wood	364.78	AF358153	
06	*B. byssicola*	Venezuela	wood	365.78	AF358154	
06	*B. byssicola*	Uganda	*Alchorea* branches	914.97	AF358151	AF358252 [m]
07	*C. rhizophaga*	?U.S.A.	?soil	100004	AF358157	
07	*C. rhizophaga*	Chile	soil	906.72a	AF358155	
07	*C. rhizophaga*	U.S.A., Ohio	root of *Ulmus americana*	202.37	AF358156	AF358225 [m]
07	*C. rhizophaga*	Switzerland	culture contaminant	361.77	AF358158	AF358228 [m]
08	*B. capitata*	Japan	bark	218.93	AF358188	AF358240 [m]
09	*C. agrawalii*	India	decomposing buffalo horn from animal house floor sweepings	533.81	AF358187	AF358241 [m]
10	*B. sporodochialis* [a]	U.S.A., Puerto Rico	bark	101921	AF358149	AF210685 [n]
11	*B. zelandiaenovae*	New Zealand	bark of *Coprosma* sp.	197.93	AF358186	
11	*B. zelandiaenovae*	New Zealand	bark of ?*Agathis australis*	100979		AF358229 [m]
11	*B. zelandiaenovae* [b]	New Zealand	bark of *Coprosma* sp.	232.80	AF358185	AF210684 [o]
13	*C. compactiuscula*	Germany	soil	729.87	AF358193	AF358242 [m]
13	*B. compactiuscula*	U.S.A., North Carolina	bark of dead *Fagus* sp.	913.97	AF358194	AF358245 [m]
13	*B. compactiuscula*	France	bark of *Fagus* sp.	592.93	AF358192	AF358247 [m]
13	*B. compactiuscula* [c]	U.S.A., Virginia	twigs of *Acer* sp.	919.97		AF210690 [o]
14	*C. rogersoniana* [d]	Brazil	soil	582.89	AF358189	AF210691 [n]
15	*B. solani*	Venezuela	decaying palm inflorescence	101926	AF358179	AF358230 [m]
15	*B. solani*	Jamaica	*Hypoxylon* sp. on bark	101924	AF358180	AF358232 [m]
15	*C. solani* f. *nigrovirens*	Netherlands	soil	183.30	AF358222	
15	*C. solani* f. *nigrovirens*	Germany	soil	223.72b	AF358223	
15	*C. solani* f. *nigrovirens*	Netherlands	tuber of *Solanum tuberosum*	229.74	AF358224	
15	*C. solani* f. *nigrovirens*	Germany	egg of *Arion ater*	142.91	AF358178	AF358244 [m]
15	*C. solani* f. *solani*	U.S.A., California		191.31	AF358176	
15	*C. solani* f. *solani*	Germany	bark	697.88	AF358216	
15	*C. solani* f. *solani*	Canada	wood	708.86	AF358175	

Table 2. Continued

	Taxon name	Origin	Substratum	Strain (CBS)	Sequence accession number of *tub*2	rDNA
15	*C. solani* f. *solani*	Netherlands	tuber of *Solanum tuberosum*	228.74		AF358243 [m]
15	*C. solani* f. *solani*	Germany	bark	752.68	AF358221	AF358246 [m]
15	*C. solani* f. *solani* [e]	France	rotten fruit of *Aesculus hippocastanum*	702.97	AF358177	AF210687 [n]
16	*B. aureofulvella*	Australia, Victoria	bark	102837	AF358220	
16	*B. aureofulvella*	Venezuela	bark of *Polylepis sericea*	200.93	AF358182	
16	*B. aureofulvella*	New Zealand	root of tree	195.93	AF358181	AF358226 [m]
17	*B. pseudochroleuca*	French Guiana	decaying palm frond	187.94	AF358174	
17	*B. pseudochroleuca*	French Guiana	decaying palm	191.94	AF358173	
17	*B. pseudochroleuca*	French Guiana	palm	220.93	AF358172	
17	*B. pseudochroleuca*	French Guiana	bark	192.94	AF358171	AF358238 [m]
18	*B. pseudostriata*	Indonesia	bark	120.87	AF358184	
18	*B. pseudostriata*	Indonesia	bark	119.87	AF358183	AF358251 [m]
19	*B. samuelsii*	Venezuela	bark	699.97	AF358190	AF358236 [m]
19	*B. samuelsii* [f]	U.S.A., Puerto Rico	bark	700.97		AF210689 [n]
20	*C. divergens* [g]	Germany	soil	967.73b	AF358191	AF210677 [o]
21	*B. ralfsii*	Australia, Victoria	bark	102845	AF358219	AF358253 [m]
21	*B. ralfsii*	Australia, Victoria	bark	102851	AF358218	
21	*B. ralfsii*	New Zealand	bark	703.97	AF358217	
21	*B. ralfsii*	New Zealand	bark	129.87	AF358195	AF210676 [o]
22	*B. epichloë*	Japan	*Sasa* sp.	101037	AF358209	AF210675 [o]
24	*C. miodochialis* [h]	Netherlands	soil	997.69	AF358210	AF210674 [o]
25	*B. pityrodes*	Mauritius	bark	102033	AF358212	AF210672 [o]
25	*B. pityrodes*	Brazil	bark	246.78		AF210673 [n]
26	*B. grammicospora*	French Guiana	standing dead tree	209.93	AF358206	AF210678 [o]
27	*B. grammicosporopsis*	New Zealand	bark of *Metrosideros* sp.	115.87	AF358204	AF210679 [o]
27	*B. grammicosporopsis*	Australia	bark	102843		AF358254 [m]
27	*B. grammicosporopsis*	New Zealand	bark of *Coprosma* sp.	111.87		AF358255 [m]
27	*B. grammicosporopsis*	Australia	bark	102834		AF358256 [m]
28	*B. subquaternata*	Venezuela	wood	107.87	AF358207	
29	*B. lucifer*	U.S.A., Puerto Rico	bark of recently dead *Casearia arborea*	100008	AF358208	AF210683 [n]
30	*B. levigata* [i]	France	branch of ?dead *Buxus sempervirens*	948.97	AF358196	AF210680 [o]
31	*C. intermedia* [j]	Netherlands	soil	508.82	AF358205	AF210682 [n]
32	*C. chlorina* [k]	Brazil	soil	287.90		AF210681 [n]
33	*B. rossmaniae*	French Guiana	bark of living liana	211.93		AF210665 [o]
33	*B. rossmaniae*	French Guiana	bark of twigs	210.93	AF358213	AF358227 [m]
38	*B. sesquicillii*	Guyana	twigs and lichen	180.88	AF358214	AF210666 [o]
39	*C. candelabrum*	Netherlands	soil	504.67		AF210668 [n]
40	*C. phyllophila*	Cuba		685.96		AF210663 [n]
40	*C. phyllophila*	France	leaves of *Viscum album*	921.97		AF210664 [o]
41	*B. setosa* [l]	U.S.A., Puerto Rico	decaying twig	917.97		AF210669 [n]
41	*C. setosa*	Cuba	*Trophis racemosa*	834.91	AF358211	AF210670 [o]
43	*B. coronata*	France	leaves of *Buxus sempervirens*	696.93	AF358215	AF210667 [o]

[a–l] given in Schroers (2000) as [a] '*Bionectria* sp. 10'; [b] '*Bionectria* sp. 9'; [c] '*Bionectria* sp. 13'; [d] 'anamorphic *Bionectria* sp. 14'; [e] '*Clonostachys* sp. 11'; [f] '*Bionectria* sp. 12'; [g] '*Clonostachys* sp. 5'; [h] '*Clonostachys* sp. 4'; [i] '*Nectria* sp. 6'; [j] '*Clonostachys* sp. 8'; [k] '*Sesquicillium* sp. 7'; [l] '*Bionectria* sp. 3'

[m] ITS-1–5.8S–ITS-2 (newly reported sequence), [n] ITS-1–5.8S–ITS-2 (reported in Schroers, 2000), [o] ITS-1–5.8S–ITS-2–LSU partial (reported in Schroers, 2000).

manually. The data were analysed by heuristic searches and optimized according to the maximum parsimony criterion, with all positions equally weighted and after a reweighting procedure according to the Retention Index.

3. (Fig. 4 a–c): A data set only comprising data from the *tub*2 gene was prepared with additional taxa of subgenus *Bionectria*, using *B. levigata* (subgenus *Zebrinella*) as outgroup. The sequence alignment was adjusted manually. The phylogenetic relationships were analysed by (i) the maximum parsimony criterion using heuristic searches and maximum tree number set to unlimited (Fig. 4 a), (ii) cluster analyses using the Neighbor-joining algorithm with maximum likelihood as distance optimization, empirical values for nucleotide frequencies, and estimated transition/transversion ratios (Fig. 4 b), (iii) maximum likelihood analyses (Fig. 4 c) using the estimated parameters found in the Neighbor-joining analyses.

4. (Fig. 5): The data set was identical to that analysed in Fig. 4 but considered only 36 parsimony-informative characters of the *tub*2 exons. The characters were analysed by heuristic searches optimized by maximum parsimony. The tree shown is the bootstrap consensus tree.

All phylogenetic analyses were done in PAUP 4.0b4a (Swofford, 2000). Heuristic tree searches that were optimized according to the maximum parsimony criterion were performed using starting trees obtained via stepwise, random sequence addition, and 1000 addition sequence replicates, tree bisection-reconnection (TBR) as swapping algorithm, 'multrees' on, and using all optimal trees for the next swapping round. The maximum tree number was set to 1000 or unlimited. The characters were unordered and equally weighted; uninformative characters were excluded from the analyses. Branch robustness was tested by heuristic searches based on 1000 bootstrap replicates (randomly sampled data sets with replacements), each with 10 replicates of random sequence addition (Figs 2, 3, 4 a, 5). In alternative searches, the characters were reweighted according to the retention index (RI) (trees not shown).

Distance analyses were done using the Neighbor-joining algorithm and maximum likelihood for distance optimization using the following parameters/assumptions: empirical values for nucleotid frequencies and an estimated transition/transversion ratio; two-parameter model variant for unequal base frequencies (Hasegawa *et al*., 1985); evolution of all variable sites at the same rate (Fig. 4 b).

Maximum likelihood analyses were performed based on heuristic searches using empirical nucleotide frequencies and a transition/transversion ratio as estimated in the Neighbor-joining analysis. The starting tree was obtained via random, stepwise addition of sequences, and 10 sequence addition replicates (Fig. 4 c).

The data were analysed with gaps coded as missing data (Figs 2, 4 b, 4 c) or after recoding selected, gap-rich positions that otherwise were parsimony-uninformative (Fig. 4 a; Table 3). Trees were rooted with basal polytomy. The recoded positions were reproduced at the end of the alignment. Character-sets (introns/exons) were defined and the DNA fragments (ITS-1–5.8S–ITS-2) were mapped in the end-block of the Paup-Nexus-file.

Abbreviations used

A.Y.R.	A.Y. Rossman
bp	base pair of nucleotide sequences
C.T.R.	C.T. Rogerson
DIC	differential interference contrast
DM	dissecting microscope
G.J.S.	G.J. Samuels
H.J.S.	H.-J. Schroers
ICBN	international Code of Botanical Nomenclature
ITS-1	internal transcribed spacer region 1 of rDNA
ITS-2	internal transcribed spacer region 2 of rDNA
K.P.D.	K.P. Dumont
LM	brightfield light microscopy
LSU rDNA	large subunit of rDNA, 28S rDNA, partial
PC	phase contrast
rDNA	ribosomal DNA
tub2	β-tubulin gene
W.G.	W. Gams

TAXONOMIC CONCEPTS AND NOMENCLATURE

GENERIC CONCEPT

The generic rank should enable inferences about natural relatedness, morphological congruence, similar ecological behaviour, and metabolite production of the classified species (Petrini, 1994). Traditionally the holomorph or the teleomorph has been used for inferences about natural relatedness, while anamorphs generally were understood to be form-genera, necessary for the identification of morphologically similar but possibly unrelated fungi (Gams, 1995). As a consequence, morphological characters of certain anamorph genera are frequently polyphyletically distributed on trees inferred from molecular data (e.g. Glenn *et al*., 1996 for acremonium-like taxa; Rehner & Samuels, 1994 for gliocladium-like taxa). While Linnaean taxonomists frequently accept paraphyletic groupings, for example if ancestral taxa need to be classified (Sosef, 1997), phylogenetic approaches accept common ancestry (monophyly) as the only grouping criterion (Hibbett & Donoghue, 1998; de Queiroz, 1996).

To cope with the pleomorphic nature of fungi, a separate naming of different morphs that belong to the same organism is permitted (Greuter *et al*., 2000: ICBN, Art. 59). Different names are used particularly for structures either formed for the sexual (teleomorph) or asexual (anamorph) reproduction of Ascomycetes and Basidiomycetes. The teleomorph can be restricted to (and is sufficiently described by) asci (spore-producing cell) and ascospores (spores purported to be the result of sexual recombination). Generally, it is the ascocarp and the ascocarp-supporting tissue that typifies a teleomorph name and the combination of such character patterns is used for its identification. Analogously, it is not only the conidiogenous cell and the conidia that characterize an anamorph but also any cell(s) developed for exposing or supporting conidiogenous cells or systems of these.

The teleomorph and the anamorph (but also morphological elements within both of these) are unlikely the product of synchronous evolution and may be influenced by the environment to an unequal degree. Classifying fungi according to the anatomical system is frequently conflicting with a natural system.

Generic concept based on teleomorphic characters.— *Bionectria* was initially described based on characters of the teleomorph and its life-style. For the type species *B. tonduzii*, Spegazzini (1919) assumed that living plant material was essential. The unispecific genus remained unrecognized until Samuels (1988a) assumed its relatedness to species of the *N. ochroleuca*-group, based on overall similarities of the crowded and warted ascocarps and the mostly 1-septate and warted ascospores.

This assumption is supported by observations made during this revision and elsewhere (Schroers & Samuels, 1997; Schroers *et al*., 1999b; Rossman *et al*., 1999). However, some species of *Bionectria* differ from others in the absence of the ascal ring, and groups of species classified here in *Bionectria* differ in perithecial wall anatomy, perithecial surface structures, stroma morphology, as well as ascospore septation and ornamentation. The presence or absence of the ascal ring in *Bionectria* is linked to the size of the ascospores (generally shorter than 15 µm in species with a ring and mostly larger than 20 µm in species without it) and possibly to differing modes of spore release. Nevertheless, most of the species classified in *Bionectria* have a conspicuous ascal ring. Its occurrence distinguishes *Bionectria* from other, closely related, genera of the *Bionectriaceae* such as *Hydropisphaera*, *Ijuhya*, and most species of *Nectriopsis*. These genera have a simple ascal tip or an apically thickened ascal wall, but lack an ascal ring even in smaller-spored species.

Morphologically, *Bionectria* is rather broadly circumscribed, which possibly is impractical for identifications. The accepted species or species groups differ in the tissue supporting the perithecia, perithecial wall anatomy, nature of the perithecial surface, as well as ascospore septation and ornamentation. To accommodate the different kinds of teleomorphic character patterns, several subgenera, namely *Bionectria*, *Astromata*, *Myronectria*, *Zebrinella*, *Epiphloea,* and *Uniparietina*, are proposed within *Bionectria*.

Molecular analyses based on rDNA sequences have shown that *Bionectria* as here delimited is a monophyletic entity within the *Bionectriaceae* (Rossman *et al*., 2001; Schroers, 2000). Relatedness of *Bionectria* taxa is also indicated by their life-style and particularly by morphological characters of the anamorphs.

Generic concept based on anamorphic characters.— The morphological feature that describes *Bionectria* best is the rather short-stiped and loosely branched secondary conidiophore that generally forms imbricate chains or columns of conidia. The secondary conidiophore unites all taxa of the monophyletic *Bionectria* and is, with the exception of *Stephanonectria* (Schroers *et al*., 1999a), not formed by other taxa of the *Bionectriaceae*.

Within *Bionectria*, however, the secondary conidiophores are differently expressed. They can be monomorphic or associated with primary conidiophores, mononematous or sporodochial, asetose or setose, contain numerous, only few, or no intercalary phialides, and their conidial masses are either white, pale orange, or green. Because of these differences, anamorphs of *Bionectria* were classified in numerous genera as described above. The use of these genera for

the classification of *Bionectria* anamorphs contradicts the interpretation that the secondary conidiophore is the unifying morphological element. The comparison of anamorphs formed on the natural substratum with those in culture as well as intergradations of character states within the genus, solves this problem. First, while *B. solani*, for example, forms distinct sporodochia on recently dead trees, conidia isolated from such sporodochia, as well as those isolated from soil may form only barely developed sporodochia or mononematous conidiophores in culture. The interpretation of *Spicaria* and *Dendrodochium* as synonyms of *Clonostachys* is based on such observations. Second, the primary conidiophores of *B. compactiuscula* occur frequently on the natural substratum while they are almost absent in culture, which could lead to a wrong classification based on the occurrence of dimorphic conidiophores in culture. The plasticity of anamorphs of these closely related species therefore may respond to the diversity of life styles, while standardized conditions may reduce the morphological diversity *in vitro*. In several species, however, primary conidiophores never were observed, while their sporodochial conidiophores are similar in overall characters to the mononematous to sporodochial secondary conidiophores of species with dimorphic conidiophores (Schroers, 2000: Fig. 6). Third, while Gams (1968) based the recognition of *Sesquicillium* on the frequent and consistent occurrence of intercalary phialides in penicillate conidiophores, *Sesquicillium* can be linked with *Clonostachys* by an almost continuous transition series including species having numerous, only few, or no intercalary phialides (Schroers, 2000: Fig. 5). It is mainly this transition series that revealed the homology of the conidiophores of the subgenera *Uniparietina* and *Epiphloea* to the secondary conidiophores of subgenera *Zebrinella* and *Bionectria*.

Chains of imbricate conidia particularly characterize the secondary conidiophores of *Bionectria*. Such chains are not formed in other, closely related genera of the *Bionectriaceae*. The chain formation is attributed to the oblique extrusion of the conidia from the phialide tip, the slightly curved shape of the conidia, and possibly to a mucilaginous coating of the conidia. Although the conidia formed on primary conidiophores are of the same shape and mostly extruded obliquely, they do not form columns but watery heads, either on solitary phialides or on whorls of adpressed phialides.

Conidia in chains of *Bionectria* are not connected to each other as in *Penicillium* or *Aspergillus* Mich. (Gams, 1978) but adhere to each other side-by-side or, rarely, end-to-end. End-to-end chains are also known in *Acremonium alternatum*, the type species of that genus, and its allies (*Acremonium* Link 'series *Terricola*' W. Gams), which belongs to the *Bionectriaceae* (Rossman *et al*., 2001). The conidia, however, are straight, and have truncate ends (Ito *et al*., 2000: Figs 4, 5). The situation therefore is not comparable to that of *Bionectria*. *Acremonium obclavatum* W. Gams (Gams *et al*., 1984), which also forms imbricate conidial chains, has clavicipitalean affinities (W. Gams, pers. comm.). Its conidial chains therefore are unlikely homologous to those found in *Bionectria*. The slightly asymmetric shape of the conidia in *Mariannaea* suggests that the imbricate conidial chains are formed by the same mechanism as in *Bionectria*. The chains, however, are in overall much longer than the columns in *Bionectria*. It is possible that imbricate conidial chains or columns allow an efficient distribution of the conidia for example by arthropods because parts of such chains may easily adhere to the bodies of the animals, be carried around, and possibly be washed off by drops of water. Thus conidial columns may have evolved independently in unrelated groups of fungi. Still, the conidial columns or chains formed by *Bionectria* species are quite unique at least within the *Bionectriaceae*.

Generic concept based on life-style.— Evidences from the life-style indicate that the species and species groups in *Bionectria* form a homogeneous group. Particularly it is the fungicolous life-style and destructive mycoparasitism that has been linked to representatives of several subgenera in *Bionectria*. Parasitic interactions of *Clonostachys* hyphae that grow around, penetrate, and eventually destroy the hyphae of unspecific fungal hosts have been found in *C. rosea* (Barnett & Lilly, 1962 and others) as well as in a strain of *Sesquicillium* (subgenus *Epiphloea;* Turhan, 1993). A mycoparasitic life-style also is indicated by the formation of perithecia, sporodochia, and conidiophores close to or on fruiting structures of fungal hosts [for subgenus *Bionectria* see Fig. 31 c and Schroers *et al*., 1999b: Fig. 5; for subgenus *Astromata* see Figs 53 a, 54 b, Möller (1901), and Samuels (1988a)]. Data today available suggest that some species of subgenus *Bionectria* may also have other biotrophic abilities including growth around roots of various living plants (Domsch *et al*., 1980), endophytic and symptom-less growth in living plants (Mueller & Sinclair, 1986), as well as destructive parasitism on animals (see 'Ecology of *Bionectria* / *Clonostachys*', pp 20, 21).

Ecological evidences may explain the diverse morphologies of the teleomorphs found in *Bionectria*. The concentration of large numbers of crowded perithecia found in the subgenera *Bionectria*, *Zebrinella*, and *Myronectria* possibly is a result of the locally restricted, densely packed mycelium of the stroma that is formed to break through the outer bark layers of recently dead trees. Conversely, the rather solitary and superficial habit of perithecia on weakly developed or even absent stromata in the subgenera *Astromata*, *Epiphloea,* and *Uniparietina* possibly is a result of the superficial and spreading growth of the *Bionectria* mycelium. Possibly the ephemeral nature of the herba-

ceous substrata neither necessitates nor allows the development of a stroma. Because ascocarps generally form a complex and frequently characteristic interface with their substrata, it is possible that environmental factors such as the nature and consistency of the host material can influence the morphology of the ascocarps and that phenotypically striking variations and adaptations of the teleomorphs even have evolved in closely related and congeneric species.

Generic concept based on DNA characters.— Based on sequence data of the LSU rDNA (Rossman *et al*., 2001), the taxa here classified in *Bionectria* form a supported clade closely related to *Stephanonectria* Schroers & Samuels, a clade comprising myxomyceticolous species of *Nectriopsis* as well as the myxomyceticolous *Sesquicillium microsporum*, *Hydropisphaera*, *Heleococcum* C.A. Jørg., *Roumegueriella* Speg., *Selinia* P. Karst., '*Nectria*' *zonata* Seaver, and *Ochronectria* Rossman & Samuels. More distantly related within the *Bionectriaceae* is a clade comprising acremonium-like anamorphs like *Acremonium alternatum* Link : Fr., the type species of *Acremonium* Link : Fr., and *Stanjemonium* W. Gams *et al*., as well as various other genera. The most distant genus included in the *Bionectriaceae* so far is *Kallichroma* Kohlm. & Volkm.-Kohlm. Inclusion of *Peethambara* and other taxa, mostly with myrothecium-like anamorphs, in the *Bionectriaceae* as suggested by Rossman *et al*. (1999) is not supported by phylogenetic analyses (Rossman *et al*., 2001).

The subgenera of *Bionectria* are only partly supported by molecular data (ITS and/or partial LSU rDNA [Schroers (2000); Rossman *et al*. (2001)]. However, these data as well as those of the *tub*2 combined with the ITS regions (Fig. 2), support the following conclusions: (i) the subgenus *Bionectria* forms a paraphyletic group, however, most of its species fall in a monophyletic clade (Fig. 2: A); (ii) the subgenera *Bionectria* and *Astromata* are closely related and form a monophyletic clade (Fig. 2: B); (iii) species of the subgenus *Zebrinella* form a distinct, monophyletic clade (Fig. 2: D); (iv) *B. pityrodes* (subgenus *Myronectria*; Fig. 2: E) and *B. setosa* (placed in subgenus *Epiphloea* based on morphological evidence; Fig. 2: F) take an isolated position within *Bionectria*; and (v) *B. coronata* is related to species of subgenus *Epiphloea* (Fig. 2: G).

SPECIES CONCEPT

Discontinuities of one or a set of morphological characters are used in this revision to demarcate taxa, mostly species. Such a concept is generally called the **morphological species concept** (Hawksworth *et al*., 1995; John & Maggs, 1997; Mayden, 1997), which is still frequently used in fungal taxonomy (Hibbett & Donoghue, 1998: Table I).

To distinguish species of *Bionectria* / *Clonostachys*, characters of the holomorph are used, which are mainly those of the sexual and the asexual fruiting structures, in addition to a few of the mycelium and cultures. In this way, the number of morphological characters is maximized for the distinction of species and a species is circumscribed by all its morphological expressions. The holomorphic approach, however, has a major disadvantage, because no teleomorph is known for several of the species, the teleomorph generally is not produced in conidial isolates, and the anamorph is frequently lacking in herbarium specimens. The taxa therefore are keyed out either according to the teleomorph (Keys 1, 3, 5) or the anamorph (Keys 2, 4, 6). However, because of numerous sibling elements found in both morphs, species identification based on only one of these morphs is not always possible.

The morphologically based species distinctions, however, are partly supported by differences in DNA-characters, particularly those of the introns of the *tub*2. The nucleotides were analyzed by optimality criteria (Figs 2–4), based on the assumption that the evolution of organisms can be traced using gene genealogies. Therefore, the concept derived from these data is close to the **phylogenetic species concept**, which defines a species as the smallest diagnosable unit of organisms within which there is a parental pattern of ancestry and descent (Cracraft, 1997).

For various reasons, the **biological species concept**, which defines a species as a group of potentially or actually interbreeding natural populations that is reproductively isolated from other such groups (Mayr & Ashlock, 1991, cited after Mayden, 1997), is not used for species of *Bionectria*. First, sexual compatibility is difficult to test in culture. When two or more strains that remain asexual in pure culture were inoculated in one Petri dish, no perithecia were detected (results not shown). Second, the formation of perithecia in culture is not necessarily a result of sexual recombination because at least a few species, particularly *B. ochroleuca*, *B. verrucispora*, and *B. grammicospora*, sometimes exhibit homothallic fruiting. Third, the relatively rare occurrence of ascomata in temperate regions indicates a predominant role of clonal reproduction of some species, lineages, or geographic populations. Fourth, for at least a few species of *Bionectria*/*Clonostachys*, no ascomata are known. Fifth, molecular tests as discussed by Taylor et al. (1999), which enable the detection of recombination events in the absence of meiosporangia, were not performed.

Because of a broad spectrum of substrata and lifestyles (see p. 20, 21), ecological characters are used as criteria for species delimitation only in a few cases. Particular ecological features, as far as known, are listed or discussed in the notes to the descriptions. In general, however, features such as destructive parasitism were linked to strains of several species but not to particular species. Furthermore, substratum specific-

ity will be difficult to assess when the primary host is a fungus and not the plant from which the ascocarps of the *Bionectria* species originate. Two *Bionectria* species, *B. coronata* on *Buxus* species and *B. verrucispora* on *Rhopalostylis sapida*, however, are only known from specific plant hosts.

NOMENCLATURE

Article 59 of the ICBN (Greuter *et al*., 2000) allows the independent naming of fungal species based on characters of either the teleomorph or the anamorph, even if characters of one of these morphs are unknown. This enables multiple generic and specific names for a particular organism. To compensate for multiple names, the ICBN rules that the earliest name typified by an element of the teleomorph covers all possible morphological expressions (holomorph) of a fungal taxon.

Accordingly, in this paper, all teleomorphs or holomorphs are classified in *Bionectria*, which is the oldest known teleomorphic genus name given to one of the species (ICBN, Art. 59.1, 2, 4). Anamorphic species, for which no teleomorph is known, are treated and classified in *Clonostachys* and their anamorph is typified by a dried culture that originated from mycelium or conidia (ICBN, Art. 59.3). Beside of naming and classifying the teleomorphs in *Bionectria*, the anamorphs of the newly described holomorph species are also named with a binominal in *Clonostachys*. This procedure is not necessary if a teleomorph is known and does not follow the recommendation in Art. 59A.3 (ICBN), however, was chosen for several reasons. First, the type of holomorphic taxa consists of only a single specimen (ICBN, Art. 8.1) that generally is the specimen with the perithecia from the natural substratum that not necessarily contains typical characters of the anamorph. By naming the species also in *Clonostachys* and supporting the name with a type, anamorphic characters eventually become fixed that frequently show more distinctive features than those of the teleomorph at species as well as generic level. Second, the connection between a teleomorph and an anamorph is corroborated nomenclatorially, particularly if dried cultures derived from ascospores of the teleomorph type specimen are used as type material of the anamorph taxon. Thus species of *Bionectria* and *Clonostachys* at least partially comprise genetically identical types and ex-type strains. From this point of view, *Bionectria* and *Clonostachys* can be considered 'synonyms'. However, under the present Code, they cannot be treated as such formally. Third, in describing the anamorphs of holomorphic species separately, not only anamorphic but also holomorphic species can be linked to a single genus, *Clonostachys*. This appears useful because there are more species described entirely on anamorphic characters than species described entirely on teleomorphic characters and because the discovery of additional taxa based on conidial isolates or the anamorph is considered more likely than based on ascospore isolates or the holomorph. By formally classifying all anamorphs in *Clonostachys*, the phylogenetic relatedness of the species are better reflected and the requirements of a botanical genus concept are practically fulfilled. To emphasize that it is the same organism that is placed in two formally different genera, the same epithets are used in *Bionectria* and *Clonostachys* for newly described holomorphic species (ICBN, Art. 59, Note 1).

This classification reflects the recent discussions on Article 59 (Seifert & Samuels, 2000; Cannon & Kirk, 2000), although it still burdens documentation with duplicate names.

ECOLOGY

Species or strains of *Bionectria*/*Clonostachys* are saprotrophs, destructive mycoparasites, lichenicoles, or inhabitants of recently dead trees and decaying leaves. Rarely they were described as parasites of myxomycetes, nematodes, ticks, molluscs, or oomycetes. Strains have rarely been isolated from water, air, or indoor environments.

The destructive, necrotrophic, and unspecific mycoparasitism of *Clonostachys rosea* (as *Gliocladium roseum*) was first described by Barnett & Lilly (1962). As mycoparasites, *C. rosea* and *C. rosea* f. *catenulata* (as *G. catenulatum*) have been tested and used as biocontrol agents against various ascomycetes, soil-borne hyphomycetes (see Domsch *et al*., 1980), and against the basidiomycete *Rhizoctonia solani* Kühn (Jager *et al*., 1979). *Clonostachys* strains have also been isolated from various basidiocarps but it is unknown whether they were saprotrophs or parasites. Generally, it is the vegetative mycelium, sclerotia, or spores that are attacked by *Clonostachys*. Three parasitic phases can often be distinguished. In phase 1 the *Clonostachys* mycelium coils around the host mycelium (Barnett & Lilly, 1962: Fig. 11; Jager *et al*., 1979: Fig. 1); in phase 2 the host mycelium is penetrated (Turhan, 1993: Fig. 1 d); and in phase 3 the *Clonostachys* mycelium grows inside the apparently killed host mycelium (Jager *et al*., 1979: Fig. 2). Pachenari & Dix (1980) described wall-degrading enzymes and a diffusible toxic substance of low molecular weight involved in the mycoparasitism.

Destructive parasitism of *C. rosea* on hosts other than fungi has been reported, for example on *Phytophthora erythroseptica* Pethybr. (Wynn & Epton, 1979), myxomycetes (Rogerson & Stephenson, 1993),

nematode eggs (Carris *et al*., 1989), and ticks (Suszkiw, 1998). A strain of *C. solani* f. *nigrovirens* killed eggs or adults of the slug *Arion ater* within a day (pers. comm. of B. Rehbein to W. Gams). The broad spectrum of hosts may indicate the potential of *Clonostachys* species to form effective but unspecific cell-wall-degrading enzymes, while the short-termed effect on *Arion ater* suggests the involvement of toxins. Few reports also describe strains of *Clonostachys* from dead animal material such as buffalo horn (*C. agrawalii*), dead insects (*C. rosea*), and horse hair (*C. candelabrum*, Domsch *et al*., 1980).

Clonostachys rosea has been isolated from various plant substrata (Domsch *et al*., 1980). It was described as wound colonizer of plants (Isaac, 1954) or senescent roots and as a systemic, endophytic invader of soybeans without causing disease symptoms (Mueller & Sinclair, 1986). Theron & Holz (1991) reported a dry decay of potato tubers caused by *C. rosea* in laboratory experiments. *Clonostachys rhizophaga* has been linked to plant-parasitic activities causing a disastrous wilting of *Ulmus americana* (Tehon & Jacobs, 1936). Comparable symptoms or other serious plant-parasitic activities, however, were not reported again for this species or for another species of *Clonostachys*. It is possible that the disease of the elms actually was caused by unrelated phytopathogenic fungi such as *Ophiostoma ulmi* (Buisman) Nannfeldt and it is possible that *C. rhizophaga* secondarily invaded the dying trees (K.A. Seifert, pers. comm.). In this revision it is purported that species of *Bionectria* / *Clonostachys* do not have serious plant-pathogenic abilities.

Another aspect of the biology of *Bionectria*/ *Clonostachys* species is their unspecific saprotrophic ability. For example, *C. rosea* is repeatedly found in numerous inventories of various soils and litter samples (Domsch *et al*., 1980). Two of the newly described species, *C. pseudochroleuca* and *C. sporodochialis* that originally were recognized as holomorphs from bark of recently dead trees, also were isolated from litter studies in tropical forests (results unpubl.; strains isolated by C. Lôpez Quintero).

While the role as saprotrophs or mycoparasites has mainly been established for conidial isolates, perithecia are mostly reported from the bark of recently dead trees or decaying leaves in mainly tropical but also temperate regions (Samuels, 1976a; Samuels *et al*., 1990). During excursions in the Luquillo Mountains of the Caribbean National Forest in Puerto Rico in 1996, ascocarps of several *Bionectria* species were found on the bark of trees that had been uprooted 7 years before by a hurricane in 1989. The description 'recently dead', which is frequently used to describe the condition of the plant substratum, possibly can be confined as a period when an uprooted tree still contains intact lignin and bark (absence of white-rot caused by basidiomycetes) with moderate moisture.

Based on sections of the ascomata and small pieces of the surrounding wood/bark, the following general observations were made: In species of the subgenera *Bionectria* and *Zebrinella*, strands or possibly continuous mats of hyphae grow subcortically below the bark. At certain spots, the filamentous cells change gradually to a prosenchymatous or pseudoparenchymatous tissue/stroma (Fig. 13 d) that breaks through the bark to form sporodochia or perithecia. In numerous cases, the stroma bearing perithecia was seated on or engulfed the subcortical fruiting structures of other fungi (Figs 31 c; 50 c, f; 53 a; 54 b, c; Schroers *et al*., 1999b: Fig. 5). The close and frequent association of the perithecial stroma and fungal host tissue supports the hypothesis that species of *Bionectria* are mycoparasites or fungicolous. It is not clear, however, whether the fungal host was dead or alive when it was contacted by hyphae of the *Bionectria* species.

Because many groups of crowded perithecia can normally be found on the same specimen (Figs 21 c; 31 a, Schroers *et al*., 1999b: Fig. 1), possibly all these groups are connected by the subcortically growing mycelium of the same homothallic strain or the same combination of heterothallic strains. Whether the subcortical mycelium of *Bionectria* continues also in parts of the tree where perithecia or conidiophores are absent is unknown. The occurrence of the *Bionectria* mycelium in most or all parts of the tree could mean that the species invades a tree before it dies and that the fungus may reproduce sexually after the death of the host tree. This hypothesis is partly supported by the results of Mueller & Sinclair (1986), who characterized a *C. rosea* strain as a symptomless but systemic colonizer of living soybeans, and by numerous studies listed in Domsch *et al*. (1980: 372, 373) that characterized *C. rosea* as a root colonizer and invader of various plants, including woody species. Provided they are harmless invaders of living plants and mycoparasites, species of *Bionectria* may play an important role as endophytes in plants and possibly as agents against fungal plant pathogens in the natural environment.

Species of the subgenera *Epiphloea, Uniparietina*, and *Astromata* mainly form superficial mycelia that produce anamorphic fruiting structures or intergrades with cells of a superficial prosenchymatous stroma or hyphae bearing perithecia. The presence of subcortical hyphae cannot be excluded. Superficial mycelium and perithecial stromata are mostly formed by *Bionectria* taxa growing on herbaceous substrata such as decaying leaves, grasses, or lichen thalli. The lack of erumpent stromata in these species groups can possibly be correlated to the ephemeral nature of the substrata (lack of time for stroma formation) or simply to the fact that an erumpent stroma is unnecessary to rupture the cortex of the plants. Differences in stroma and ascocarp morphology between the species groups or subgenera in *Bionectria* can possibly be explained as adaptations to the different nature of the host plants (see 'Generic concept based on life-style'; also Schroers, 2000).

MORPHOLOGY

MORPHOLOGICAL CHARACTERS

Stroma or tissue supporting the perithecia.— In *Bionectria* a stroma can be present or absent, of various morphology, and with diverse stroma/perithecial wall interfaces. A stroma erumpent through bark generally arises from hyphal cells (Fig. 13 b, d) that run subcortically parallel to the surface of the substratum. In species of subgenus *Bionectria*, the erumpent stroma consists of angular (Fig. 11 f), pseudoparenchymatous cells that sometimes contain vacuoles. The cells of the stroma and those of the outer perithecial wall region are morphologically indistinguishable and show an indistinct interface (Figs 21 h, 24 d, g). Species of the subgenera *Myronectria* and *Zebrinella* have a similar erumpent stroma but their cells are prosenchymatous, hyphal, and generally orientated vertically (Figs 59 e, 64 h, 67 d). In species of subgenus *Zebrinella*, the interface of the stroma and wall regions is discontinuous (Fig. 73 b), while in species of subgenus *Myronectria*, hyphae of the stroma apparently are continuous with the middle perithecial wall region [Fig. 59 e; arrow in Fig. 4 h (Schroers, 2000)]. No developed stroma was observed in subgenus *Astromata*, where the perithecia are generally connected by hyphae to the substratum, sometimes a putative fungal host (Figs 53 a, 54 b, c). The stroma in spp. of subgenera *Epiphloea* and *Uniparietina* is superficial and densely hyphal or epidermoidal (Figs 76 d, 79 c, 83 c, 96 b, 99 b). The cells of the stroma are not continuous with any of the perithecial wall regions but apparently merge with the outermost cell layer of the perithecial wall.

In species of the subgenera *Bionectria*, *Zebrinella*, and *Myronectria*, the numbers of perithecia on each stroma vary but frequently reach or exceed 100 (Figs 21 c, 31 a). In the other subgenera, perithecia are aggregated to gregarious to solitary (Figs 53 a, 78 a, b).

Perithecial shape and collapse of dry perithecia.— Perithecia of *Bionectria* are globose or somewhat higher than wide. In dense aggregations of somewhat spherical clusters, the perithecia can also be widest in the upper part, and thus obovoid to somewhat pyriform (Fig. 18 d, h). The most simple perithecium, however, is that of *B. coronata*, which is ampulliform because of its globose main body and a somewhat papillate ostiole (Fig. 96 a).

Factors such as perithecial wall anatomy, perithecial shape, and connection to the substratum or stroma, or uneven thickness of the perithecial wall, may determine whether perithecia collapse when dry. Mostly they collapse laterally or have a slight apical pinching, for example in species where the perithecia are broadly connected to the stroma as in *B. kowhaii* or *B. ralfsii* (Figs 13 a, c, 50 a, c). Large warts also may influence pinching, particularly when apical warts are larger than those formed laterally; such perithecia may appear pinched only in the lateral part near the perithecial base. The general occurrence of lateral pinching distinguishes *Bionectria* at least from the closely related *Hydropisphaera* and *Ochronectria*, where the perithecia collapse apically to form cups (Rossman *et al*., 1999: Plate 4 b for *O. calami*). The perithecia of *Ochronectria* are relatively firmly and broadly connected to the substratum and those of *Hydropisphaera* are mostly wider than high.

Perithecial pigmentation.— No structure of the ascocarps (or the anamorph) of *Bionectria* gives a KOH reaction, but ascocarps may become slightly paler in lactic acid. The colour of the perithecia is generally orange, yellowish orange, or brownish orange, rarely brownish. Generally it is the outer and inner perithecial wall region that is pigmented. Perithecial warts generally are less pigmented, off-white tan, or pale yellow (Schroers & Samuels, 1997: Figs 2–5). The darker wart-free ostiolar region generally contrasts against the pale-coloured warts (Figs 6 a, 27 a, 64 a, b; Schroers & Samuels, 1997: Fig. 3). The ostiolar region, however, frequently is more intensely pigmented, also in species with smooth perithecia (Schroers & Samuels, 1997: Figs 2, 4). The 'orange' colour apparently is located in the walls of cells of the outer perithecial wall region and in intracellular drops that, however, were not observed in all species and not in all specimens of one species. After observation of very many specimens, the following features were found to be discontinuous and significant: Perithecia of *B. samuelsii* are rather brownish orange and entirely smooth; those of *B. sporodochiella* are more yellowish and have similarly coloured small warts; those of *B. ochroleuca* are light orange and rough; those of *B. verrucispora*, *B. aureofulvella*, and *B. solani* are light orange and entirely smooth; those of *B. apocyni* are brownish orange and have small, less pigmented warts; those of *B. pseudostriata* are brownish and entirely smooth; in most species of subgenus *Epiphloea* they are light orange and smooth; those of *B. setosa* are rather brownish. Pigmentation, however, can be influenced by the age of the perithecial stroma and young or immature ascocarps may be more yellowish, while in old and overmature material they tend to be brownish. All observations are described from ascocarps that were at least air-dried. Colours of the perithecia and also their warts generally are slightly more intense after rehydration in water.

Perithecial wall anatomy.— The perithecial walls can consist of different kinds of cells that form distinct regions. The term region is used for one or several layers

of morphologically similar cells. Characters of the regions are observed (i) in median, longitudinal sections and (ii) in squash mounts by the varying focus of the microscope on the regions that run parallel to the surface (subsurface view in optical section). Three distinct regions were observed.

The **innermost region** is morphologically identical in all taxa. Its cells are flat or somewhat acerose when seen in section (Fig. 24 f) and mostly lobed to oval in subsurface view (Figs 46 k; 94 g). The cell walls appear uniformly thick in sections but are unevenly thickened in subsurface views. The very thin parts of the wall that are restricted to defined spots look like pores (Fig. 46 k) and have been called 'pseudopores' (Schroers *et al*., 1999b). Their function is unknown. The layers of these cells completely surround the perithecial cavity and continue into elongate cells that line the ostiolar pore of the perithecium (Figs 18 e; 46 d). Subapically, the cells merge inward into brick-like, thin-walled cells, which bear the periphyses of the ostiolar canal (Fig. 46 d; Schroers *et al*., 1999b: Fig. 9). In lateral and basal parts of the perithecium, similar cells that are flat in sections and subcircular to oval in subsurface view (Fig. 47 a, b) support the asci that extend into the perithecial cavity (Fig. 18 e). In species of subgenus *Uniparietina*, only this single region is developed (Fig. 96 b). All other subgenera form additional regions outwards. The ampulliform shape of the perithecia of *B. coronata* is obviously correlated with the lack of additional regions. Most other perithecia have an ampulliform (Figs 21 f; 31 d) or broadly ampulliform perithecial shape if the inner region is considered alone (Fig. 67 c). It is mainly the outer wall region and the perithecial warts that determine the overall appearance of the perithecial shape.

Because the inner region can be found in all three families of the *Hypocreales*, whether additional regions are present or not, this region is regarded as the perithecial wall *sensu stricto* (Schroers *et al*., 1999b). Similar cells with unevenly thickened walls and 'pseudopores' have been illustrated for example in *Cosmospora* (*C. joca* (Samuels) Rossman & Samuels, Samuels *et al*., 1991: Fig. 23; *C. lasiodiplodiae* (Samuels) Rossman & Samuels, ibid.: Fig. 25; *C. pseudepisphaeria* (Samuels) Rossman & Samuels, Rossman *et al*., 1999: Plate 28i), *Pseudonectria rousseliana* (Rossman *et al*., 1993: Figs 9, 10), and species of *Nectriopsis* (reviewed in Schroers *et al*., 1999b, p. 379). Interestingly, similar cell shapes were also described in the outer cleistothecial cell layer of the unrelated *Emericella bicolor* M. Christensen & States (*Eurotiales*) (Christensen *et al*., 1978). In all these cases, this structure was observed in the outermost cell layers of the perithecial wall, which indicates that these species only have a single wall region and lack additional regions that are mostly present in the taxa studied here. Cells of additional outer regions are either distinct derivatives of the inner region or non-homologous to the cells of the inner region. The outer wall region of *Bionectria* is non-homologous with the inner region because a hyphal middle region separates them, at least in subgenus *Bionectria*.

A clearly distinguishable **middle wall region** is observed in the subgenera *Bionectria* and *Myronectria*. It consists of one or several layers of hyphae forming a *textura intricata* (Figs 14 a, 46 j, 59 h). The region is mainly visible in the lateral and subapical parts of the perithecial wall and apparently does not continue into the basal part (Fig. 24 g). It is covered in all parts by an outermost wall region and does not penetrate into the apex of the perithecium (Fig. 46 d). During sectioning, the perithecial wall frequently ruptures along this hyphal region (Fig. 46 g). The hyphal cells separate the cells of the outer and the inner regions. Therefore it is unlikely that the cells of the outer perithecial wall region are derivatives of the inner one. The hyphal region is easily observed in subsurface view, while it is hardly recognizable in sections by round cells outlining the cell lumina (Figs 31 f; 44 c).

In the *Bionectriaceae*, perithecia sometimes are embedded in hyphae or hyphae arise from the perithecial wall (e.g. *Protocreopsis* Doi, *Nectriopsis*). In *B. coronata* (subgenus *Uniparietina*) hyphal setae arise from the area surrounding the ostiole (Fig. 96 c; Juel, 1925: Taf. 1, 2). In all these cases the perithecial wall consists only of a single region. It can be speculated that these hyphae are homologous to those of the middle region of *Bionectria*.

The **outermost region** of the *Bionectria* perithecia consists of angular to globose cells that form a *textura angularis* or *globulosa*. Such an outer region is present in all subgenera expect *Uniparietina*. The shape of the cells of the outer region distinguishes the subgenera to a certain extent: In the subgenera *Bionectria* (Fig. 40 f, j; exception: *B. sporodochialis*: Fig. 24 e and *B. ralfsii*: Fig. 50 j) and in species of subgenus *Epiphloea* (Fig. 76 f, g), the cells are angular and the walls of adjacent cells are firmly connected. In species of the subgenera *Zebrinella*, *Astromata* and *Myronectria*, as well as in *B. sporodochialis* and *B. ralfsii* (subgen. *Bionectria*), the cells at least of the outer layers are globose to subglobose (Figs 54 d, 59 f, 62 d, 67 e) and appear loosely aggregated. In these taxa, the walls of adjacent cells typically are not firmly connected throughout and leave some free space in between (e.g. Fig. 59 f).

As mentioned above, the main outer wall regions in the subgenera *Epiphloea* and *Bionectria* are similar. However, species of subgenera *Epiphloea* and *Uniparietina* form an additional outermost cell layer, which is absent in the other *Bionectria* species. This cell layer, visible mainly in surface view, consists of diffuse sometimes epidermoidal cells (Figs 78 f, 79 f, 96 d) that apparently continue into the stromal base.

In species of subgenus *Bionectria*, the perithecial surface can be smooth, rough, or warted. In species of the subgenera *Zebrinella*, *Myronectria*, and *Astromata*

perithecia are typically warted, except for *B. levigata* (subgenus *Zebrinella*) with smooth perithecia. Perithecia of subgenera *Epiphloea* and *Uniparientina* are always smooth.

Perithecial warts if present are strongest developed in the upper part of the perithecia. They can be irregularly scattered (Fig. 21 a) or radiate from the perithecial apex downwards (Figs 18 b, 64 b). The warts formed in subgenus *Zebrinella* typically taper slightly towards the tip as seen in longitudinal sections (Figs 62 b; 64 d; 69 c), while they are broadly rounded in other subgenera.

The cells of perithecial warts do not differ principally from those of the main outer region (Figs 18 g, 27 f, 54 d, 62 b, d). Perithecial warts are therefore regarded as a derivative of the outer region. The cells of their bodies normally are uniformly thin-walled, while marginal cells frequently have unevenly thickened walls, particularly in species of the subgenus *Bionectria*. The thickest wall is directed outward and is particularly seen in the warts surrounding the ostiole (Figs 21 d, g, 54 d, j). In contrast to subgenus *Bionectria*, the cells of the warts in subgenus *Zebrinella* are typically uniformly thin-walled. The cells of the latter subgenus mostly become smaller towards the tip of the warts, which at least is less obvious in the other subgenera (Figs 62 b, 64 d, 67 b, 69 b).

The absence of warts and/or cells with unevenly thickened walls also is typical of certain species or species groups within one subgenus. In subgenus *Bionectria*, all species forming *Clonostachys solani*-like anamorphs have smooth perithecia mostly lacking cells with unevenly thickened walls, while those with *Clonostachys rosea*-like anamorphs are mostly rough or warted, and have cells with unevenly thickened walls.

Perithecial walls in *Bionectria* spp. are generally rather thick, soft, and fleshy, thus similar to those of related genera such as *Ochronectria* and *Hydropisphaera*. The thickness of the perithecial wall, however, varies in species of *Bionectria* because of diverse dimensions of the outer and inner wall regions, and presence or absence of perithecial warts. The walls in the subgenera *Uniparietina* and *Astromata* are rather thin, resembling other genera of the *Bionectriaceae* such as *Nectriopsis*, *Nectriella*, and *Mycocitrus*. Perithecial warts and cells with unevenly thickened walls are mostly absent in other genera of the *Bionectriaceae*. Instead, in other genera of the *Bionectriaceae*, structures such as hyphal fascicles (as in *Ijuhya* and *Hydropisphaera*) or swollen or elongated cells (as in *Stephanonectria*, *Nectriella*, *Clibanites* or *Pronectria*) can be observed, particularly around the ostiole. Wart structures similar to those seen in *Bionectria* spp. are found mainly in the *Nectriaceae*, for example *Albonectria rigidiuscula* (Berk. & Broome) Rossman & Samuels (Rossman *et al*., 1999: Plate 25 d) and *Nectria s.s*. The perithecial warts can therefore be considered typical of *Bionectria* to a certain extend.

Asci.— Asci are similar in shape and structure in the taxa treated but vary in size. Length and width ranges more or less correlate with the size ranges of the ascospores. Asci are typically clavate, apically rounded (Figs 13 f, 25 a, b) to flat (Figs 47 c, d, 54 i, 85 h), or sometimes have prominent edges (Fig. 9 a), subapically thickened walls (Figs 9 a, 40 g), and an apical ring (Figs 21 i, 29 i, j, 65 a, 85 h). The ring formation apparently depends to some degree on the size of ascospores. The ring is generally clearly visible in species with relatively short ascospores (to 20 µm). Species with relatively large ascospores do not form a ring, as in subgenus *Myronectria* (Fig. 60 a), or form a ring that can be seen in immature but is more or less invisible in mature asci, as in *B. apocyni* (Fig. 9 a) or *B. lucifer* (Figs 69 g, 70 a). The presence of well-developed ascal rings in small-spored species and their poor development or absence in large-spored species possibly can be linked with alternative mechanisms of spore release. Large ascospores possibly are released through ascal rupture or evanescent ascal walls, while short ascospores may be released through the apical ring. The absence of a ring can therefore be interpreted as a loss or reduction and should have limited taxonomic relevance for *Bionectria*. However, neither apically intact nor disrupted asci could be observed after spore discharge.

In numerous specimens, mainly of species of subgenus *Bionectria*, sterile, thin-walled, broadly clavate, disintegrating structures were observed among the asci, with a size range similar to that of the asci (Figs 25 b, 31 g, 47 b). Schroers *et al*. (1999b) interpreted these elements as paraphysis-like cells. Because they generally appear connected to the ascal hymenium and because of their apically free ends, these structures may present non-functional asci that disintegrate into part-cells. Because they occur next to immature but fully intact asci and they do not have traces of an apical ring (Fig. 31 g), these disintegrating structures are unlikely the remains of asci after spore release.

Ascospores.— The ascospores generally are ellipsoidal and taper slightly towards their ends. Bean-shaped ascospores particularly characterize *B. pityrodes* (subgenus *Myronectria*, Fig. 60 b).

Species of *Bionectria* generally have 1-septate ascospores. Only in *B. coronata* the ascospores are aseptate. The rare occurrence of 2- and 3-septate ascospores in *B. tonduzii* and *B. apocyni* (not shown) is interpreted as the result of a secondary process in the maturation of relatively long spores. Multiseptate ascospores never have been observed inside mature asci. The transverse septum generally divides the ascospores in *Bionectria* into two equal cells. Constriction at the septum frequently is observed in discharged ascospores but disarticulation into part-spores was never observed.

Ascospores are warted in species of the subgenera *Bionectria* (Figs 7 b, 8 h, 18 k, 29 f) and *Astromata* (Figs 54 h, 56 i); distinctly striate (Figs 62 h, 67 i, 69 i) or rarely smooth (Fig. 72 b) in species of subgenus *Zebrinella*; smooth in species of the subgenera *Myronectria* (Fig. 60 b) and *Uniparietina* (Fig. 97 b); and variably ornamented, smooth or warted (Figs 78 h, 79 j), with warts arranged in striae (Fig. 85 i), or with ± intricately arranged short striae (Fig. 76 k) in species of subgenus *Epiphloea*.

The warts of the ascospores of *B. verrucispora* are conspicuously thick. They are particularly visible when mounted in water and lactic acid (Fig. 29 e, f), but disappear when mounted in KOH (Fig. 29 l, m). The chemistry of the warts, therefore, may be different from that of the ascospore wall, which remained intact in KOH. The ascospores are smooth in early states of their development in the asci (Figs 9 a, 31 g, 44 i, 65 a) and become ornamented later, while still in the asci (Figs 25 b, 29 j). Using phase contrast microscopy, a bright halo surrounding the ascal ascospores is generally observed (Figs 9 a, 25 b, 29 j, 31 g, 65 a, 92 e) that sometimes appears as a distinct layer sheathing the still aseptate ascospores (Fig. 44 i). It is possible that the ascospore ornamentation of *Bionectria* derives or results from a transformation of sheaths differing in chemical composition from the ascospore walls.

Conidiophores.— Conidiophores have been defined as a system of one or several conidiogenous cell(s) plus any differentiated supporting cells (Pirozynski, 1971). Terms used here for the description of the conidiophores are taken from Seifert (1985) who partly adopted them from Pitt (1979). Conidiophores of *Bionectria* are rarely simple and acremonium-like, generally differentiated into a stipe and a branched part (*penicillus*). The stipes typically arise erect from a submerged supporting hypha, a solitary aerial hypha or aerial hyphal fascicles, ropes or strands. The stipe consists of one or several cells and is always delimited by a septum near the base. The branched part can be a single whorl of phialides (*monoverticillate*), several whorls of phialides arising from intercalary cells of the main axis (*2*- or *more-level verticillate*, Seifert, 1985: Fig. 3 f), or it consists of successive branches that form whorls of additional supporting cells or whorls of phialides (*biverticillate*, *terverticillate*, etc.). The latter structure matches the situation in *Gliocladium s.s*. or most *Penicillium* species and also is called *gliocladium-like*. The compact more-level verticillate and the regularly, for example, terverticillate branching patterns are referred to as *penicillate*. Only for simple-branched conidiophores with divergent supporting cells and divergent phialides the term *verticillium-like* is used. Cells supporting the phialides are generally called *metulae*, although they are not differentiated from other branches.

Conidiophores in *Bionectria*/*Clonostachys* frequently are dimorphic, which means that two types can occur in the same strain, sometimes formed close together on the same hyphal strand (Fig. 36 f). For the two kinds of conidiophores, the terms 'primary' and 'secondary' are adopted (Gams, 1984). While primary conidiophores are always mononematous, the secondary conidiophores can be mononematous, loosely aggregated, or distinctly sporodochial within the same strain. In certain species secondary conidiophores are entirely sporodochial. Sporodochia are generally best developed on the natural substratum but weakly produced or lacking in culture. The terminology adopted here uses (i) the nature of the conidiophores (primary *vs*. secondary; mononematous *vs*. sporodochial) and (ii) similarities of the conidiophores to those of genera that are here synonymized with *Clonostachys*, or to the conidiophores found in unrelated genera, viz. clonostachys-, dendrodochium-, sesquicillium-, acremonium-, verticillium-, gliocladium-, or myrothecium-like (Table 1).

Setae and sterile elements of conidiophores and sporodochia.— Setae associated with the conidiophores have been observed in four species of subgenus *Epiphloea* (Figs 90 b, 93 b, 95 c; Samuels, 1989: Fig. 36). Setae arise either from the mycelium close to the conidiophores, from the penicilli, or from near the stipe base of the conidiophores. The setae are ± indistinguishable from the cells of the conidiophores in width and wall thickness, but taper ± continuously in the upper part. In other hypocrealean genera, setae or sterile extensions are common in conidiophores, such as *Hypocrea* (*Trichoderma* sect. *Pachybasium*) (*Hypocreaceae*), *Nectricladiella* Crous & C.L. Schoch (*Cylindrocladiella* Boesew.), *Calonectria* De Not. (*Cylindrocladium*), *Leuconectria* Rossman, Samuels & Lowen (*Gliocephalotrichum* J.J. Ellis & Hesselt.), *Pseudonectria* (*Volutella*), *Cosmospora* (*Volutella*) (all *Nectriaceae*), and *Myrothecium* (*Bionectriaceae*). Conidiophores with setae in *Bionectria* have a similar branching pattern as in *Cylindrocladium* or *Cylindrocladiella* but terminal vesicles were never observed.

Phialides.— Conidiogenous cells in *Bionectria* are phialides. A periclinal wall thickening is generally visible. Phialides of primary conidiophores are almost cylindrical but taper gradually, particularly in the upper part. Sometimes a short collarette is recognizable (Fig. 22 c). Phialides of the secondary conidiophores are narrowly flask-shaped, widest in the lower third and then taper slightly and continuously toward the ± truncate tip (Fig. 9 c). The conidia produced from these phialides generally are slightly curved, frequently have a somewhat flattened side, and a laterally displaced hilum. In *B. samuelsii* (subgenus *Bionectria*) and *B. pityrodes* (subgenus *Myronectria*), the phialides are more cylindrical or expand slightly apically until

they taper rather abruptly immediately below the tip. The phialide tip therefore seems to be rounded (Figs 47 e, 60 c, 61 d). The conidia produced from these phialides only show a slightly laterally displaced hilum (Fig. 47 f) or are symmetrical (Fig. 61 g).

Intercalary phialides with a cylindrical neck are usually formed in each branch of a whorl, sometimes interspersed with terminal phialides (Fig. 77 c). They typically support a single terminal phialide (Fig. 86 c). Rarely two or three intercalary phialides are formed below each other (Fig. 97 c). In contrast to other genera such as *Nectria* (Seifert, 1985: Fig. 30 e, g–j), intercalary phialides are restricted to the apical part of the penicillus in *Bionectria* species. They are rare in species of subgenus *Bionectria*, more common in subgenus *Zebrinella*, and typical of the subgenera *Epiphloea* and *Uniparietina*. The phialide(s) above intercalary phialides sometimes collapse in rather young conidiophores, leaving behind the intercalary phialide with the short conidiogenous neck (Fig. 34 b).

Conidial aggregation.— The round conidial heads on primary conidiophores have a watery consistence and collapse easily when touched with a glass needle. The heads are generally hyaline or hardly pigmented. Conidia on secondary conidiophores are often arranged in imbricate chains, in which the conidia are attached side by side or at least slightly overlapping (Figs 32 a, b, 57 d, 87 i). Conidia are formed in chains on solitary phialides or in complex columns on adpressed penicilli. In sesquicillium-like conidiophores, conidiation from intercalary phialides also contributes to the formation of conidial columns (Fig. 84). The orientation and the density of the phialides determine the size and shape of the conidial columns. Slender and often long conidial columns are formed from adpressed whorls of phialides or penicilli, while penicilli with divergent branches and less adpressed phialides tend to form broad and rather short columns. Conidial columns do not collapse when touched with a glass needle, and may remain stable in certain species even in old colonies. On complex, more divergently branched conidiophores and aggregates of conidiophores, conidial columns collapse earlier to form dome-shaped slimy masses. It is assumed that a slimy matrix keeps the conidia in chains or columns; slime production appears strongest on sporodochia. Conidia are more or less hyaline in all species except *B. ralfsii* (Fig. 51 c–f). It is likely that the orange or green hues of conidial masses, particularly of sporodochial species, originate from the slimy matrix.

Conidial shape, pigmentation, and septation.— Conidia of *Bionectria* spp. are ± ellipsoidal to subfusiform (L/W *ca* 2–4). Typically they are slightly curved, have one somewhat flattened side, and a laterally displaced hilum (Fig. 23 c), particularly in species of the subgenera *Bionectria* and *Epiphloea*. In species of the subgenera *Zebrinella* and *Myronectria* the conidia are almost straight with an almost median hilum (Fig. 74 f) or are entirely symmetrical without a visible hilum (Figs 67 k, 70 d). In species of subgenus *Astromata* the conidia have a somewhat protruding hilum, but resemble those found in subgenus *Bionectria*. In *B. coronata* the conidia are almost fusiform without forming a visible hilum. The distal ends of the conidia are broadly rounded, tapering, or aculeate, sometimes differing among closely related species (e.g. *B. apocyni*, *B. oblongispora*, and *B. kowhaii*: Figs 10 e, 12 e, 15 d).

Conidial curvature and displacement of the hilum are the result of an oblique extrusion of the conidial initial from the phialide tip (Fig. 16 b). The form of the conidia obviously also determines their imbricate arrangement. All species with curved conidia and laterally displaced hila form imbricate chains or columns from the secondary conidiophores. The fact that the conidial chains in species of subgenus *Zebrinella* are only poorly developed or quickly collapse is possibly a result of the almost straight conidial shape. The lack of columns on primary conidiophores might be because of the watery consistency of the masses or to a more straight conidial extrusion from the phialide aperture (Fig. 19 c), which, however, was seen clearly only in *B. byssicola*.

Conidia of *Bionectria* are hyaline or greenish hyaline; conidial masses are mostly lightly coloured, salmon, yellowish, or green. Only *B. ralfsii* has darkly pigmented conidia that are not translucent in microscopical preparations. In KOH, the green conidial masses change to olive-green to brown and back to green after addition of lactic acid. This reaction is considered of low relevance because it was observed also in species of *Myrothecium* sensu Tulloch (1972) and *Trichoderma*. The intensity of pigmentation is light-dependent. Particularly after incubation under near-UV light, deeper orange hues were observed that occur only in older colonies under day-light. The pigmentation of the agar medium was similarly affected by light (reviewed in Schroers *et al*., 1999b).

Conidia of *Bionectria* are smooth, which is the most frequently encountered pattern in hypocrealean fungi. The few exceptions with ornamented conidia are found for example in *Peethambara* (*Bionectriaceae*), *Myrothecium cinctum* (Corda) Sacc. and certain species of *Trichoderma* (*Hypocreaceae*).

Conidia of *Bionectria* are aseptate. Only in *B. setosa* and *B. gibberosa* 1-septate conidia are found infrequently (Fig. 93 c; Vittal, 1974: Fig. 1 F).

POLARITY AND EVOLUTION OF CHARACTER STATES

Some character states change gradually within *Bionectria*, allowing the detection of certain transformation series and the development of hypotheses on character state polarizations.

The number of intercalary phialides formed in the secondary conidiophores changes gradually within *Bionectria*. Intercalary phialides are frequently and consistently formed by species of the subgenera *Epiphloea* and *Uniparietina* and are absent or rare in species of the subgenera *Bionectria*, *Astromata*, and *Myronectria*. The subgenus *Zebrinella* comprises species either without or with low numbers of intercalary phialides and at least one species with rather high numbers of intercalary phialides.

The lack or the infrequent formation of intercalary phialides is manifested in species of the subgenera *Bionectria* and *Myronectria* that have a mycelial growth below the bark of recently dead trees and that form erumpent stromata in order to break through the bark to form sporodochia and perithecia. In contrast, species of the subgenera *Epiphloea* and *Uniparietina* that form intercalary phialides abundantly do not form erumpent stromata and sporodochia but have gregarious or solitary perithecia on ephemeral herbaceous substrata (see 'Generic concept based on life-style'). Apparently a shift of life-style from herbaceous to woody substrata is correlated with an increased tendency to form erumpent stromata, sporodochia, and crowded perithecia and a decreased tendency to form intercalary phialides. Similar trends are found in the formation of dimorphic conidiophores. While conidiophores of the subgenera *Epiphloea* and *Uniparietina* are mostly monomorphic, those of the core group of subgenus *Bionectria* consistently are dimorphic.

The subgenus *Zebrinella* is intermediate between both groups. Its species form erumpent stromata bearing groups of perithecia as in subgenus *Bionectria*, however, no sporodochia are found. While intercalary phialides are formed abundantly in some of its species, they are rare or absent in others. A conidiophore dimorphism can be found in some of its species, but is weakly pronounced or absent in others.

Bionectria coronata (subgenus *Uniparietina*) is the most deviating species in *Bionectria* because of its simple perithecial wall and aseptate ascospores. It is classified in *Bionectria* because of the secondary conidiophores that are similar to those of the subgenera *Epiphloea* and *Zebrinella* (Schroers, 2000: Fig. 5). *Bionectria coronata* possibly contains ancestral character states that could be used to polarize some of the transformation series described above for three reasons. First, characters could have evolved from simple to complex and the aseptate ascospores and the simple perithecial wall of *B. coronata* can be interpreted as simple. Second, while most species of *Bionectria* are non-specific saprotrophs or parasites, *B. coronata* is exclusively known from *Buxus*, either as an endophyte (Luginbühl & Müller, 1980), parasite (Farr *et al.*, 1989), or as a saprotroph on dead, mostly fallen leaves. According to Cooke and Whipps (1980), a specific nutritional mode and a link to a particular host can be interpreted as ancestral, from which necrotrophism or saprotrophism could have evolved. Third, the host genus *Buxus* is considered relatively old [fossils as old as 136 million years are known (Strasburger, 1983)] and, based on 18S ribosomal DNA analyses (Soltis *et al.*, 1997), *Buxus* occupies an isolated position within the angiosperms. Several other fungi are only known from *Buxus*, for example *Pseudonectria rousseliana* (Mont.) Wollenw. (anamorph *Volutella buxi* (Corda) Berk.), *Ceuthospora buxi* (Fr.) Petrak, *Marasmius buxi* Fr., *Rosellinia buxi* Fabre, *Nectria desmazierii* Beccari & De Not. (anamorph *Fusarium buxicola* Sacc.), and *Hyponectria buxi* (Alb. & Schwein. : Fr.) Sacc. This plant host obviously has a highly specific and probably conserved fungal biota. In assuming that host–fungus relationships are phylogenetically of similar age as that of the host, it is possible that these fungi have maintained certain ancestral traits.

Based on these assumptions, ascospores of *Bionectria* species could have evolved from aseptate to 1-septate, perithecia from astromatous to stromatous, life-style from leaf-inhabiting to bark-inhabiting and from plant-parasitic to saprotrophic or unspecificly mycoparasitic, conidiophores from monomorphic to dimorphic, and intercalary phialides from common to rare or absent.

Table 3. Recoding of selected otherwise parsimony-uninformative characters of the *tub*2 (used in Fig. 4 a).

Taxon	Indel	Character code used for the indel	Position in alignment
B. aureofulvella (CBS 195.93, 200.93)	CTT	1	65–67
B. solani (CBS 708.86, 191.31, 697.88, 702.97, 752.68, 101924, 101926)	CTT	1	
C. solani f. *nigrovirens* (CBS 183.30, 223.72b, 229.74, 142.91)	CTT	1	
B. pseudochroleuca (Ja-On Park No. 4680)	GTT	2	
All others	– – –	0	
B. byssicola (CBS 914.97, 101918, 293.78, 365.78)	T	1	163
B. apocyni 130.87	A	2	
All others	–	0	
C. rosea f. *rosea*, conidial isolates (CBS 710.86, 704.97, 100502, 912.97, 117.23, 376.55, 438.68, 226.48)	GAT	1	471–473
B. ochroleuca, ascospore isolates from temperate regions (CBS 406.95, 194.57)	GAT	1	
C. rosea f. *catenulata*, conidial isolates (CBS 154.27, 126.72, 221.72b)	GAT	1	
B. ochroleuca, ascospore isolates from tropical regions (CBS 193.94, 916.97) and all others	– – –	0	
B. samuelsii	C– –	2	

DESCRIPTION OF MOLECULAR DATA AND TREES

The amplified region of the *tub*2 gene was *ca* 1500 bp long. A 5'-part of *ca* 600 nucleotides that included three introns was sequenced (Fig. 1). The lengths of the exons were constant in all sequences obtained and the introns were located at conserved places of the gene. The intron lengths differed among the *Bionectria* taxa (intron 1: 159–179 bp; intron 2: 63–77 bp; intron 3: 155–158 bp). Length differences were compensated in the alignments by gaps. Several of these gap positions resulted in uninformative characters that were excluded in parsimony analyses. Three of the parsimony-uninformative indels, of 1–3 nucleotides, were replaced by additional symbols, because they were located in a conserved area and appeared characteristic for particular strains or species (Table 3). Independent of their length, these indels were interpreted as single events. The recoded indels were considered in the parsimony analysis of the data set analysed in Fig. 4 a.

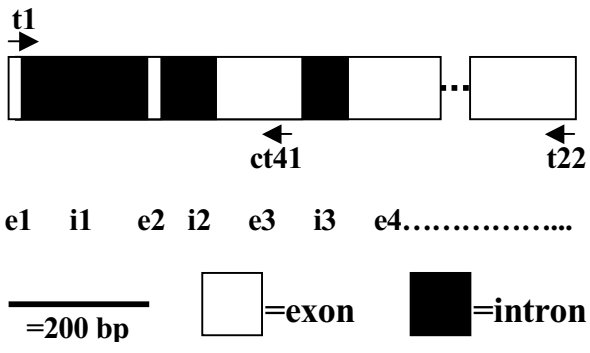


Fig. 1. Map of the partial *tub*2 showing the relative positions of the amplification primers (t1 and t22), the sequencing primers (t1 and ct41), the four exons (e1–e4), and the three introns (i1–i3).

Besides variations of nucleotides in the third position of the coding DNA triplets, which had no consequences for the amino-acid phenotype, some variations were found in the first 2 positions that resulted in changed amino-acids (Table 4).

The length of the ITS-1 varied between 155 and 158 nucleotides, the length of the 5.8S rDNA was always 158 nucleotides, and the length of the ITS-2 varied between 167 and 170 nucleotides.

Qualitative differences and length variations of *tub*2-introns caused problems in the alignment of the sequences, particularly when representatives of different subgenera were compared (Fig. 2). The alignment of the data set for Fig. 2 was based on an automated multiple alignment for reproducibility. Because of the heterogeneity of the introns, low gap opening and gap extension penalties were used and transitions were scored as mismatches (p 13). The tree obtained by parsimony analysis of a combination of *tub*2- and rDNA (ITS-1–5.8S–ITS-2) sequences has a topology similar to the tree based entirely on rDNA data (ITS-1–5.8S–ITS-2–LSU *ca* 500 bp) (Schroers, 2000) but emphasizes the segregation of subgenus *Zebrinella* more strongly (Fig. 2: D, bootstrap score: 98). The subgenus *Astromata* is highly supported (Fig. 2: C), however, it does not form a monophyletic lineage in *Bionectria* but is paraphyletic (Fig. 2: C). The relatedness of *Bionectria coronata* (subgenus *Uniparietina*) (Fig. 2: G) to subgenus *Epiphloea* (Fig. 2: F) is at least weakly supported in this analysis), in common with inferences from rDNA (Schroers, 2000). *Bionectria pityrodes* (subgenus *Myronectria*; Fig. 2: E) is unrelated to the other subgenera, although it forms crowded perithecia

Table 4. Examples of amino-acid changes in the *tub*2 because of mutations in the first or second position of the DNA-triplets.

Taxon	Strain (CBS)	DNA triplet (compared with that of other species)	Amino-acid (compared with that of other species)	Amino-acid position
B. coronata	696.93	GGC (AGC or AGT)	Gly (Ser)	37
B. epichloë	101037	AGC (AAT or AAC)	Ser (Asn)	33
B. epichloë	101037	GGT (GCC or GCT)	Gly (Ala)	54
B. grammicosporopsis	115.87	GGT (AGC or AGT)	Gly (Ser)	37
B. levigata	948.97	GGT (AGC or AGT)	Gly (Ser)	37
B. pityrodes	102033	GGA (AGC or AGT)	Gly (Ser)	37
B. ralfsii	129.87	AGC (AAT or AAC)	Ser (Asn)	33
B. ralfsii	129.87	AAT (AGC or AGT)	Asn (Ser)	37
B. ralfsii	129.87	GCC (TCC or TCT)	Ala (Ser)	55
B. rossmaniae	210.93	GGT (AGC or AGT)	Gly (Ser)	37
B. sesquicillii	180.88	GGC (AGC or AGT)	Gly (Ser)	37
B. sesquicillii	180.88	AAC (TCC or TCT)	Asn (Ser)	55
C. miodochialis	997.69	AGT (AAT or AAC)	Ser (Asn)	33
C. miodochialis	997.69	GGT (GCC or GCT)	Gly (Ala)	54

on erumpent stromata (as in subgenera *Bionectria* and *Zebrinella*) and a hyphal, middle perithecial wall region (as in subgenus *Bionectria*).

Because of ambiguities in the alignment of Fig. 2, additional analyses (Figs 3, 4) only consider species in subgenus *Bionectria* using *B. levigata* (subgenus *Zebrinella*) as outgroup, excluding representatives of other subgenera. Several nucleotide changes also were found within some of the supported clades. This is indicated by the long terminal branches of species in subgenus *Zebrinella* (average terminal branch length: 38 steps) and the subgenera *Uniparietina*/*Epiphloea* (average terminal branch length: 48 steps). Somewhat shorter terminal branches are found in the strongly supported clade that comprises species of subgenus *Bionectria*, all of which form dimorphic conidiophores (average terminal branch length: 15 steps).

Heuristic parsimony searches on the combined dataset analysed in Fig. 3 resulted in six equally parsimonious trees that were based on 227 parsimony-informative characters. In these trees the positions of *B. apocyni*, *B. kowhaii* (both always clustering together), *B. oblongispora*, and *B. zelandiaenovae* differed. While *B. oblongispora* always clustered close to *B. sporodochialis*, the doublet *B. apocyni* / *B. kowhaii* either formed a clade with both of them or clustered at the base of a clade comprising *B. ochroleuca*, *B. byssicola*, *C. rhizophaga*, *B. sporodochialis*, and *B. oblongispora*. *Bionectria zelandiaenovae* clustered either with *C. agrawalii* and *B. capitata* or formed a solitary branch between these and *B. pseudostriata*. The tree shown (Fig. 3) has the same topology as the single tree obtained in heuristic parsimonious searches using weighted characters according to the Retention Index (not shown).

Within subgenus *Bionectria*, most nucleotide differences were found in the sequences of *B. compactiuscula* (Fig. 3, 4: G), and those of species of a clade comprising *C. rogersoniana*, *B. samuelsii*, and *C. divergens* (Fig. 3: H), and *B. ralfsii* (Fig. 3: I). All these species, clustered outside a well-supported clade comprising homogeneous species of the subgenus *Bionectria* (Figs 2, 3: A). Of these species, *B. compactiuscula* and *C. rogersoniana* form dimorphic conidiophores, which are typical of the closely related species of the subgenus *Bionectria* (Figs 2, 3: A), and *B. compactiuscula* forms a teleomorph that matches those of species of subgenus *Bionectria*. *Bionectria compactiuscula* and *C. rogersoniana* fall within the subgenus *Bionectria* because of their morphology despite their molecular distinctness. The other species, *B. samuelsii*, *C. divergens*, and *B. ralfsii*, are morphologically heterogeneous in characters of the conidiophore branching pattern and conidial size and shape, and in few characters of the teleomorphs.

Within subgenus *Bionectria*, the branching patterns of the conidiophores that define the *Clonostachys rosea*- or the *C. solani*-complexes are distributed paraphyletically. *Clonostachys rosea*-like primary conidiophores with divergent phialides are formed by *B. byssicola*, *C. rhizophaga*, *B. ochroleuca*, and the unrelated *C. agrawalii*, *B. capitata*, and *B. zelandiaenovae*; *Clonostachys solani*-like primary conidiophores with adpressed phialides are formed by *B. solani*, *B. aureofulvella*, and the unrelated *B. pseudostriata*.

Heuristic searches on *tub*2 sequences (Fig. 4 a) resulted in 144 equally parsimonious trees based on 213 parsimony-informative characters. After reweighting the characters according to the retention index, 18 trees were retained (not shown) that differed (i) in the relative positions of the strains in the *B. solani*-clade (Fig. 4 a: K), where *C. solani* f. *nigrovirens* and the tropical isolate of *B. solani* (CBS 101926) always grouped together, and (ii) in placing the strains of *B. pseud-*

Table 5. Tree statistics.

Tree optimization	Figure and data set	Number of included characters	TL [a]; – Ln L [b]	CI [c]	HI [c]	RI [c]	–Goloboff fit	Number of trees
MP [d]-BS [d]	Fig. 2 [e]	378/1243	1444 [a]	0.458	0.542	0.572	246.760	1
MP	Fig. 3 [e]	227/1136	646 [a]	0.546	0.454	0.675	169.185	6
MP	Fig. 3 [e, f]	227; 57 with weight 1; 170 with weight < 1	209.1 [a]	0.729	0.271	0.852	81.794	1
MP-BS	Fig. 3 [e]	227	672 (353–1255) [a]	0.525	0.475	0.646	166.075	1
MP	Fig. 4 a [g]	213/1136	659 [a]	0.537	0.463	0.712	155.527	144
MP	Fig. 4 a [f, g]	213; 49 with weight 1; 164 with weight < 1	225.5 [a]	0.695	0.305	0.841	77.743	18
MP-BS	Fig. 4 a [g]	213	693 (354–1414) [a]	0.511	0.489	0.680	151.650	1
NJ-ML [d, h]-BS	Fig. 4 b [i]	641	4883.24845 [b]					1
ML [h]	Fig. 4 c [i]	641	4858.81622 [b]					1
MP-BS	Fig. 5 [j]	36	150 [a]	0.307	0.693	0.464	21.804	1

[a] TL = Tree length.
[b] – Ln L = – Ln likelihood.
[c] CI = consistency index; HI = homoplasy index; RI = retention index.
[d] MP = maximum parsimony; BS = bootstrap analysis; NJ = Neighbor-joining; ML = maximum likelihood.
[e] Combined data from *tub*2 and rDNA (ITS1-5.8S-ITS2); only using parsimony-informative alignment positions.
[f] Data reweighted according to the Retention Index.
[g] Data from *tub*2 (exons & introns); parsimony-informative alignment positions plus recoded characters listed in Table 3.
[h] Empirical nucleotide frequencies: A: 0.19, C: 0.27, G: 0.24, T: 0.30; estimated transition/transversion ratio: 1.8.
[i] Data from *tub*2 (exons and introns); all alignment positions without character coding.
[j] Data from *tub*2, parsimony-informative alignment positions of exons only.

ochroleuca in a monophyletic or a paraphyletic group (Fig. 4 a: L). Two other inferences based on the Neighbor-Joining algorithm (Fig. 4 b) and maximum likelihood optimization (Fig. 4 c) differed from the parsimony analysis (Fig. 4 a) (i) in the position of *C. rhizophaga* (Figs 4 a–c: M), which either was close to *B. byssicola* (Figs 4 a, c: N) or to *B. oblongispora*, *B. kowhaii*, and *B. apocyni* (Fig. 4 b: O); (ii) in the phylogeny of *B. byssicola* (Figs 4 a–c: N), which either is monophyletic (Fig. 4 b: N) or paraphyletic (Figs 4 a, c); and (iii) in the phylogeny of *B. pseudochroleuca* (Figs 4 a–c: L). The species clade of *B. ochroleuca* (Figs 4 a–c: P) is divided into two subclades comprising either ascospore- or conidial isolates. The subclade with the conidial isolates comprised strains of *C. rosea* f. *rosea* and *C. rosea* f. *catenulata*, of which several strains had identical sequences. The close affinity of both varieties is bootstrap-supported, but the strain CBS 443.65 (ex-type strain of *Gliocladium roseum* var. *viride*) and strain 438.68 (conidial isolate forming perithecia in homothallic condition) are excluded from the supported branch. The strains of the clade comprising the ascospore isolates were more variable. The subclade received middling bootstrap-support [values 75, 72 (Figs 4 a, b)]. Strong bootstrap-support was obtained for the clade that comprised all strains including ascospore- as well as the conidial isolates [values 90, 96 (Figs 4 a, b: P)]. Three species with relatively long conidia, *B. oblongispora*, *B. kowhaii*, and *B. apocyni* (Figs 4 a–c: O), appear to be closely related, however, they are not monophyletic but paraphyletic.

Clonostachys solani-like species form two unrelated groups. The first clade is that of the closely related *B. solani* and *B. aureofulvella* (Figs 4 a–c: S). In the species clade of *B. solani* (Figs 4 a–c: K) the tropical ascospore isolate CBS 101926 always clustered together with *C. solani* f. *nigrovirens*, both being nested among other strains of *B. solani* / *C. solani* f. *solani*. The second clade containing a species with a *C. solani*-like anamorph, *B. pseudostriata*, is more close to *B. zelandiaenovae*, *C. agrawalii*, and *B. capitata*. These species form a statistically unsupported group (Figs 4 a, c: Q) or a paraphyletic group (Fig 4 b: Q).

Based on 36 parsimony-informative alignment positions of the *tub*2 exons, high support was only found for the species clade of *B. ochroleuca* (Fig. 5) including conidial isolates with both white and pale orange as well as greenish conidial masses.

Additional tree statistics are given in Table 5.

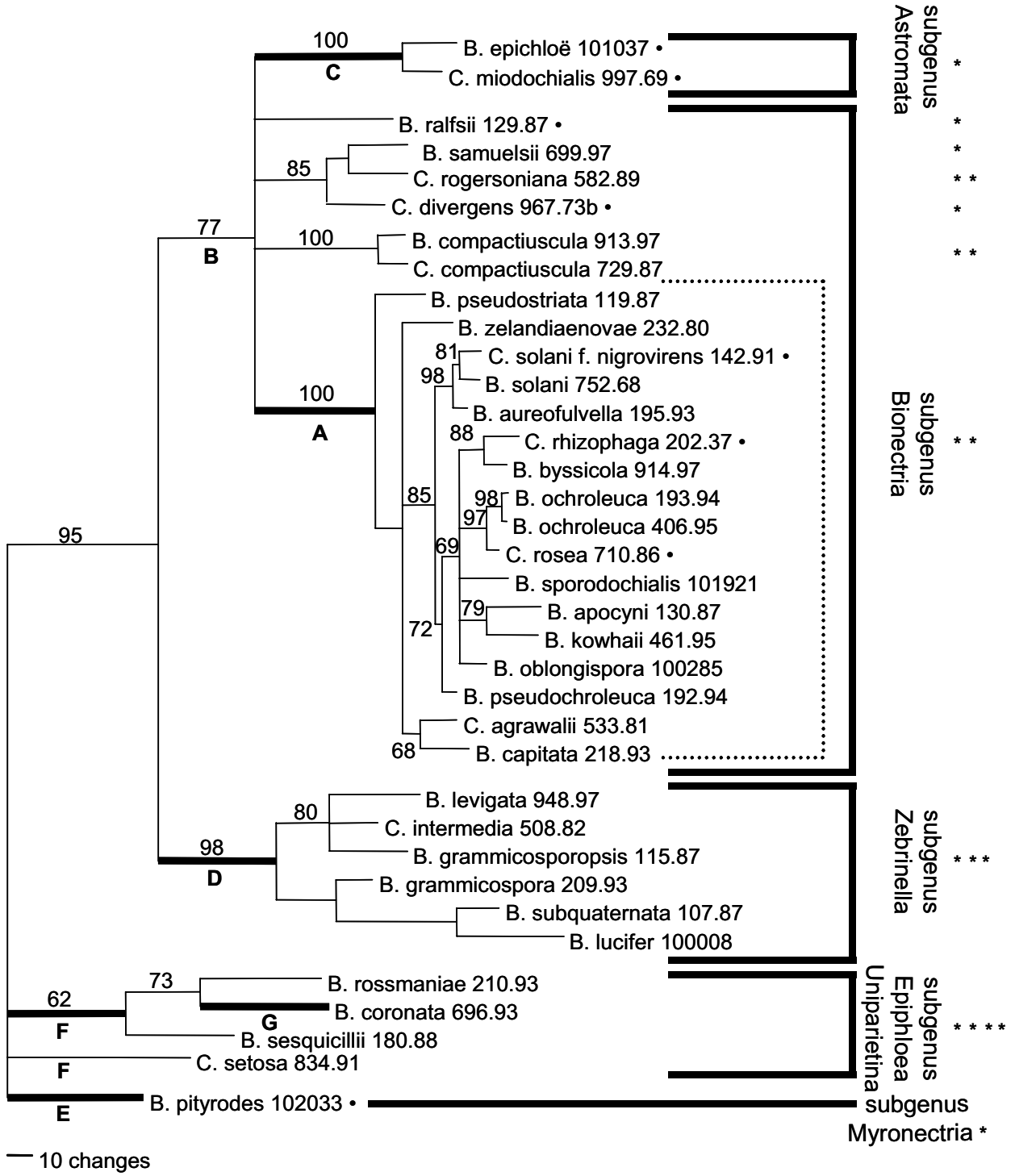


Fig. 2. Bootstrap consensus tree of most parsimonious trees: heuristic searches based on 1000 bootstrapped data sets sampled from combined *tub*2- and rDNA (ITS1–5.8S–ITS2) sequences, showing relationships of the subgenera within *Bionectria*. Bootstrap values higher than 60 are shown. **A** and species between **A** and **C:** Subgenus *Bionectria* of the genus *Bionectria*. Two of its species with dimorphic conidiophores, *B. compactiuscula* and *C. rogersoniana* cluster outside clade A. Species with entirely sporodochial anamorphs (*B. samuelsii*, with brownish orange conidial masses; *B. ralfsii*, *C. divergens*, with greenish conidial masses) are distributed among species with sporodochial and mononematous, dimorphic conidiophores. **B:** Subgenus *Bionectria*, in relation to paraphyletic subgenus *Astromata* (**C**). **D:** Subgenus *Zebrinella*. **E:** Subgenus *Myronectria* (*B. pityrodes*). **F:** Subgenus *Epiphloea*. **G:** Subgenus *Uniparietina*. Points (•, right of strain number) indicating species with green-pigmented conidial masses scattered among taxa with white to pale-orange, non-green conidial masses. Asterisks (right of clades) indicating occurrence of intercalary phialides: **** intercalary phialides abundantly formed below solitary phialides; *** intercalary phialides frequent but less constantly formed and/or lacking in some species; ** intercalary phialides infrequent, rare, or absent; * intercalary phialides not seen.

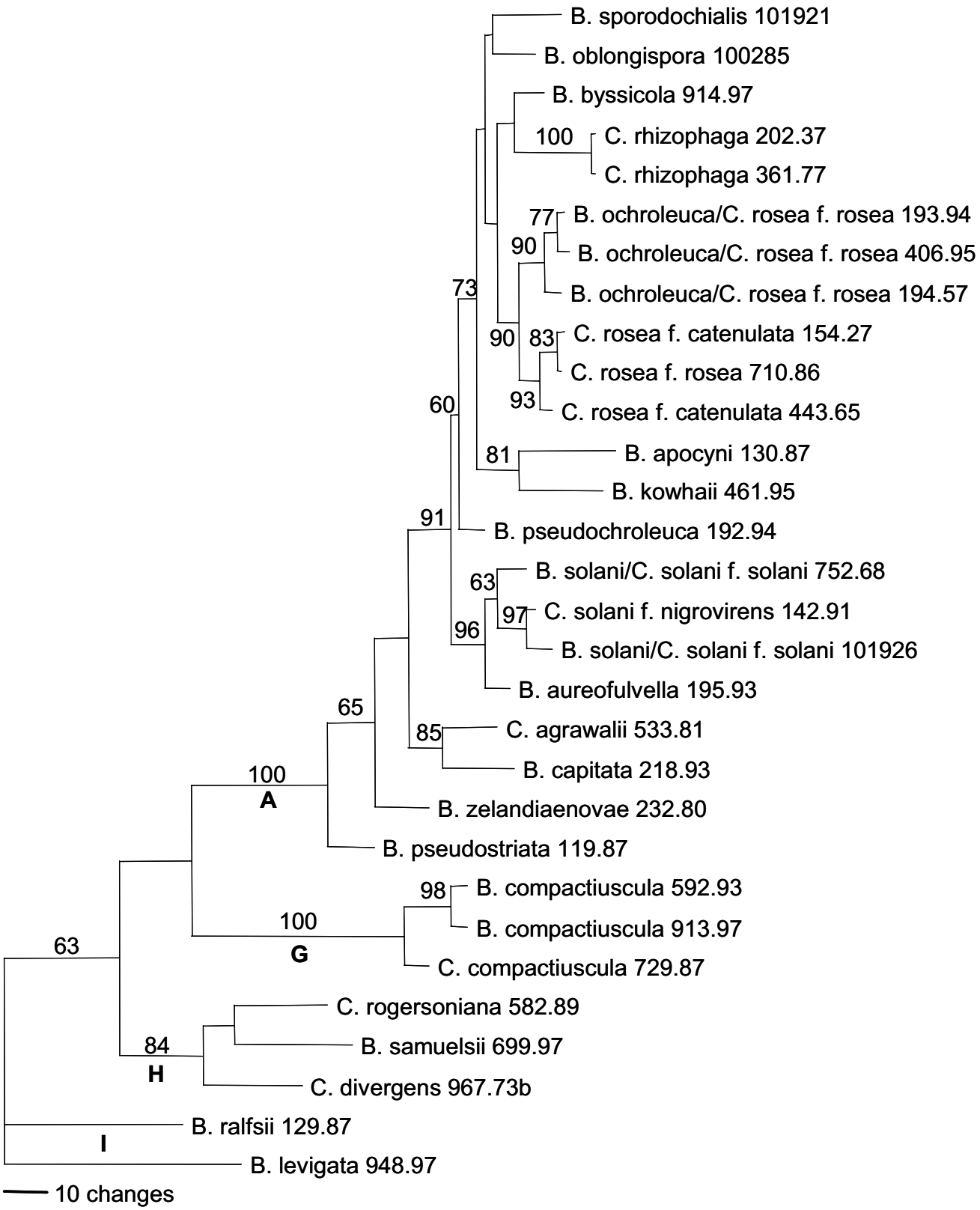


Fig. 3. One of 6 most-parsimonious trees obtained by heuristic searches based on combined parsimony-informative data of the *tub*2 (exons and introns), and ITS1–5.8S–ITS2 (rDNA), showing relationships of taxa within subgenus *Bionectria*. The tree shown has a branching pattern identical to the single most-parsimonious tree that was received after characters were re-weighted according to the retention index. Bootstrap values higher than 60 derived from 1000 resampled data sets are shown. Letters below the branches are explained in the text.

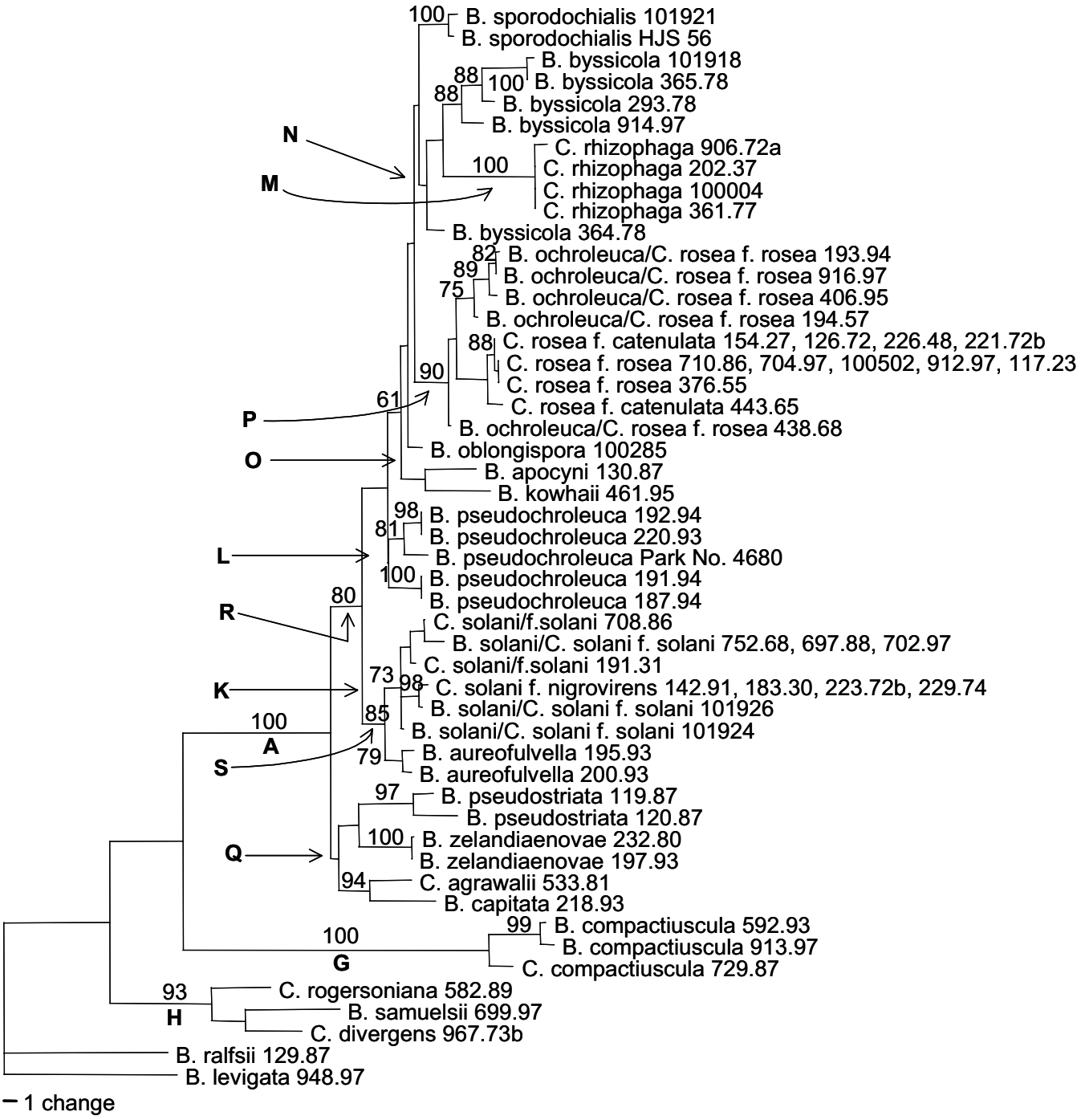


Fig. 4 a. One of 144 most-parsimonious trees obtained by heuristic searches based on parsimony-informative data of the *tub*2 (exons and introns), using the recoded data listed in Table 3, showing relationships of taxa within subgen. *Bionectria.* The tree shown has a branching pattern identical to the consensus tree of 18 most-parsimonious trees obtained after reweighting the characters according to the retention index (RI). Bootstrap values higher than 60 derived from 1000 resampled data sets are shown. Letters inserted next to the branches are explained in the text.

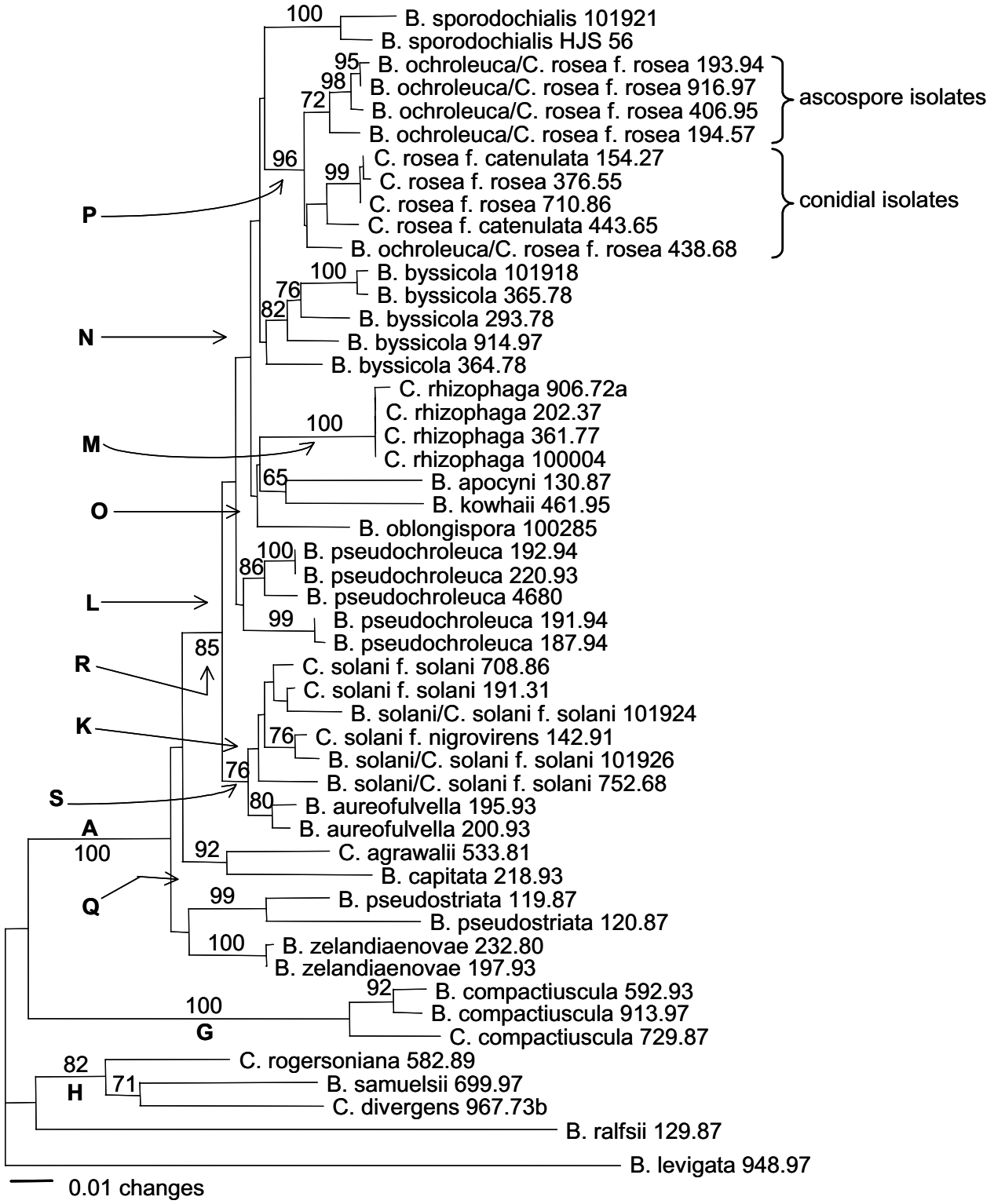


Fig. 4 b. Neighbor-joining tree based on all data of the *tub*2 (exons and introns), using maximum likelihood as distance optimization, empirical values for nucleotide frequencies, and an estimated transition/transversion ratio, showing relationships of taxa within subgen. *Bionectria*. Bootstrap values higher than 60 derived from 1000 resampled data sets are shown. Letters inserted next to the branches are explained in the text.

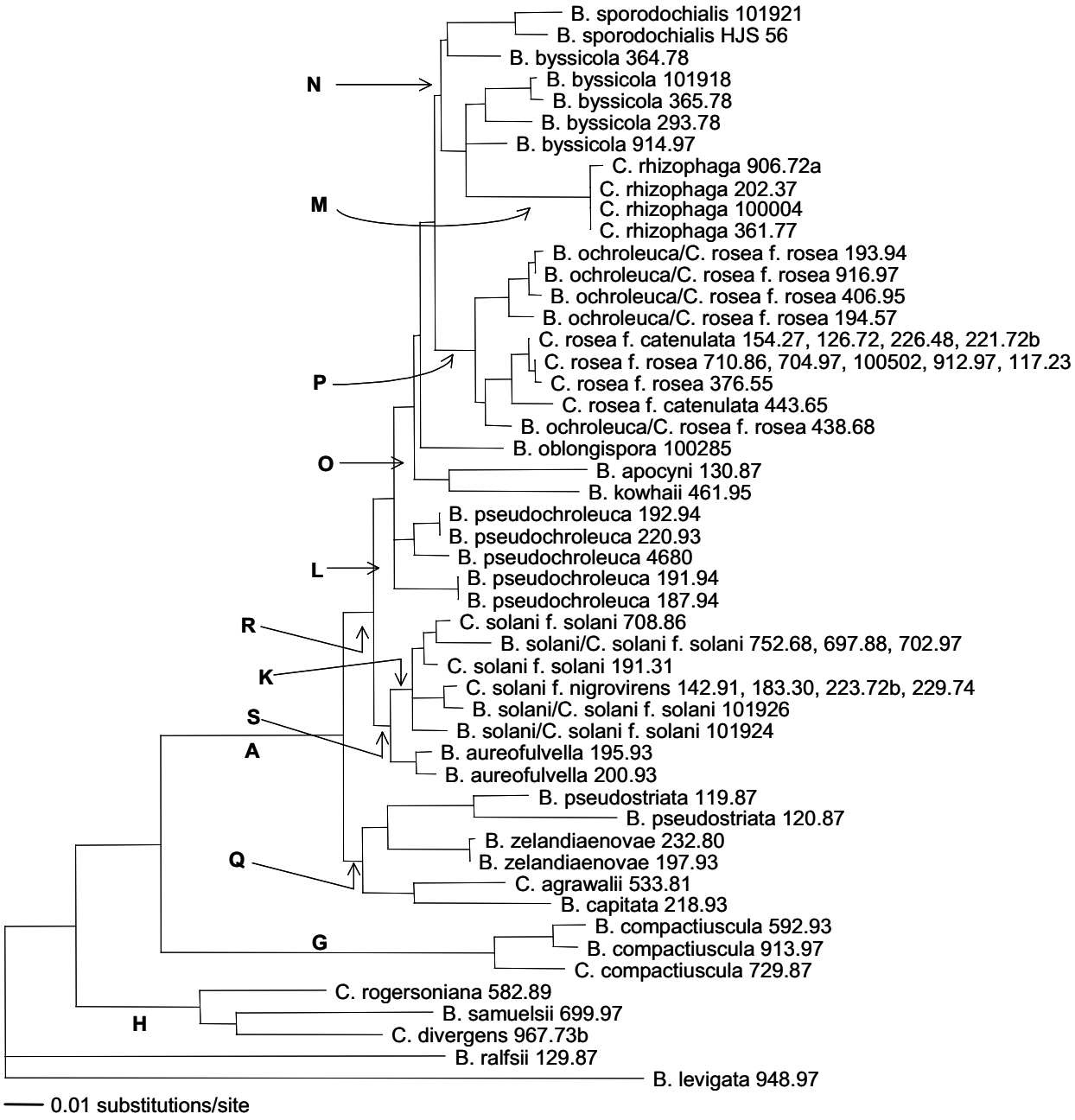


Fig. 4 c. Maximum likelihood tree based on all data of the *tub*2 (exons and introns), using the nucleotide frequencies and the transition/transversion ratio as obtained in the analyses of Fig. 4b, showing relationships of taxa within subgen. *Bionectria*. Letters inserted next to the branches are explained in the text.

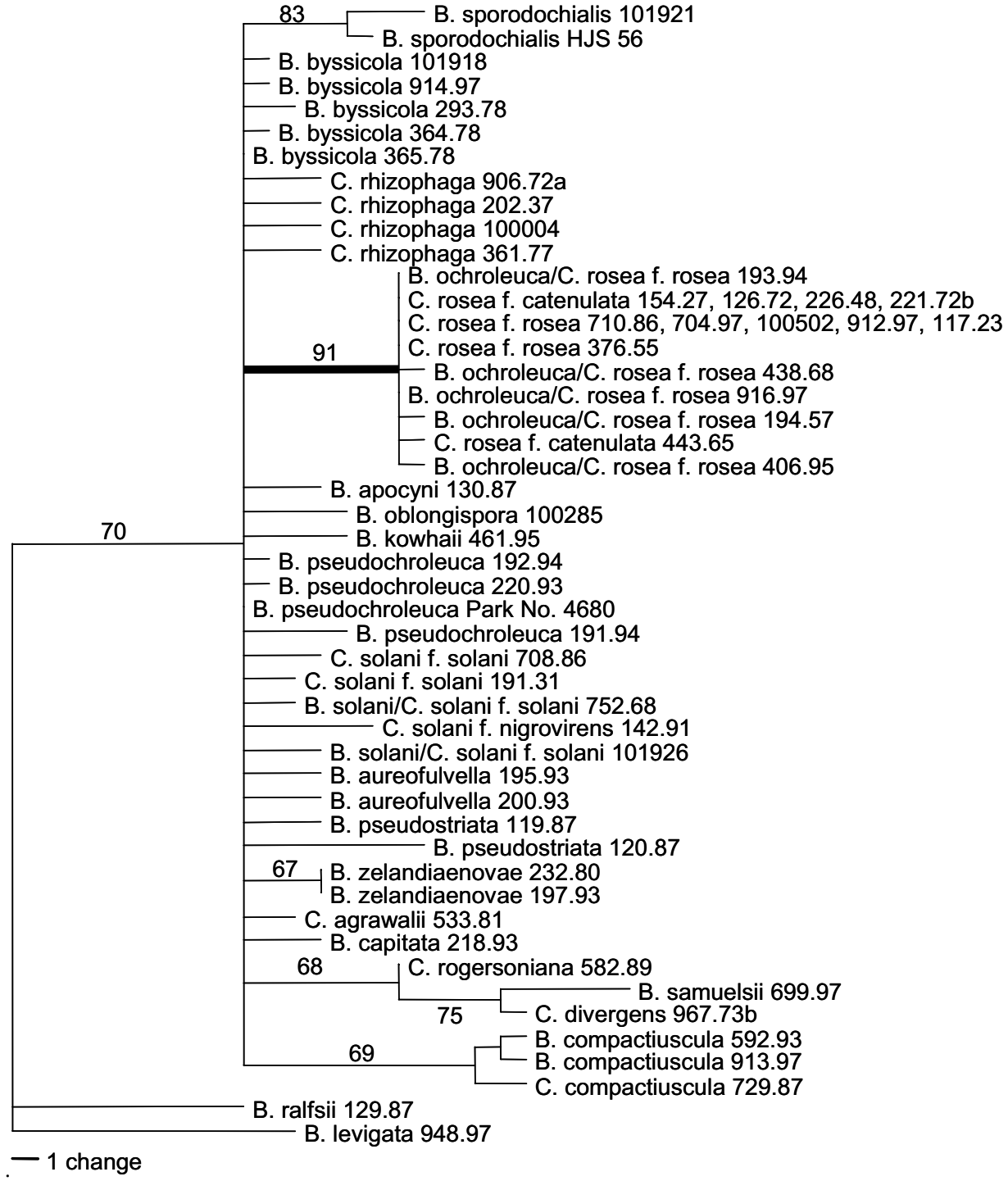


Fig. 5. Bootstrap consensus tree from heuristic parsimony searches based on 36 parsimony-informative characters of the *tub*2 exons. Bootstrap values higher than 60 derived from 1000 resampled data sets are shown. Beside a few others, mainly the *Bionectria ochroleuca* clade is statistically supported.

DICHOTOMOUS KEYS

1. Key to genera mainly of *Bionectriaceae* with superficially free perithecia, based mainly on characters of the ascomata

1 Perithecia partly embedded in an effused stroma, hyphal stroma, or at least partly surrounded by prosenchymatous stroma, generally densely aggregated; perithecial wall of 1 region; ascospores 1-septate **2**

1 Perithecia not embedded in or surrounded by a stroma, or embedded or surrounded only near the base, with or without hyphae arising from the perithecia, solitary, gregarious, or densely aggregated, crowded; perithecial wall of 1–3 regions; ascospores 0- to multiseptate **4**

2 Cells embedding the perithecia hyphal, frequently branched **3**

2 Cells embedding the perithecia dense, pseudoparenchymatous to prosenchymatous, angular to subglobose, partly forming short chains, or somewhat prosenchymatous ..... ***Stilbocrea*** Pat. (anamorph *Gracilistilbella* Seifert) (Rossman *et al*., 1999)

3 Mainly on dead monocotyledonous plants; perithecia almost completely embedded by the hyphal stroma; asci narrowly clavate; ascospores ellipsoidal to fusiform, tapering at both ends, smooth to striate ..... ***Protocreopsis*** Doi (anamorph acremonium-like) (Rossman *et al*., 1999)

3 On myxomycetes; perithecia embedded by the hyphal stroma in the lower part; asci mostly cylindrical; ascospores broadly ellipsoidal, ends frequently somewhat truncate, smooth to warted ..... ***Nectriopsis*** Maire *sensu stricto* (anamorph acremonium-like) (Samuels, 1973); if perithecia superficially free and anamorph *Rhopalocladium*, see *Nectriopsis sporangiicola*

3 Mostly on basidiomycetes (*Stereales, Poriales, Agaricales*, *Boletales*), rarely on discomycetes; perithecia on intertwined or compact hyphae (subiculum) or almost embedded in a hyphal stroma; asci cylindrical; ascospores frequently fusiform, each end apiculate, or ellipsoid to lanceolate with rounded ends, smooth or warted ..... ***Hypomyces*** (Fr.) Tul. (*Hypocreaceae*) (anamorphs *Cladobotryum*, *Sepedonium*, *Mycogone*, *Stephanoma*, or acremonium-, verticillium-, papulaspora-like; Rogerson & Samuels, 1989; 1993; 1994)

4(1) Free-ending hyphal elements, tooth-like cells, setae, or triangular spike-like fascicles arising from the perithecia **5**

4 Free-ending elements lacking; perithecia smooth or warted because of cells similar to those of the perithecial wall **13**

5 Free-ending elements more or less restricted to the ostiolar region; perithecial apex frequently crown-like (elements arranged vertically) or apically flat (elements arranged horizontally) **6**

5 Free-ending elements not confined to the ostiolar region, or predominantly arising from the lateral part of the perithecium; perithecial rounded or papillate, not flat or crown-like **10**

6 Free-ending cells near the ostiole hyphal, solitary, not tooth-like, without swollen end-cells, ± thin-walled **7**

6 Free-ending cells near the ostiole arranged in fascicles if hyphal, or tooth-like, or clearly wider than the cells of the perithecial wall, sometimes with swollen end-cells, sometimes thick-walled **8**

7 Growing on plant material such as dead leaves or twigs; setae surrounding the ostiole forming an inconspicuous crown, 0- or few times septate, slightly undulate, to 40 µm long ..... ***Bionectria*** subgenus ***Uniparietina*** (anamorph *Clonostachys*, sesquicillium-like or unknown; two species included: *B. coronata* (43) known only from *Buxus* in temperate regions and *B. aurantia* (44) known only from Indonesia)

7 Mainly fungicolous; setae, if present, shorter, not undulate ..... '***Nectriopsis***' (anamorphs diverse) (Samuels, 1988a) see also entry 15

8 Free-ending hyphae densely aggregated to triangular fascicles, spike-like, arising from near the ostiole, to more than 200 µm long ..... ***Ijuhya*** Starbäck (anamorph acremonium-like) (Rossman *et al*., 1999)

8 Free-ending hyphae not arranged in fascicles **9**

9 Cells surrounding the ostiole tooth-like, 5.5–19 × 2.5–10 µm, densely arranged, thick-walled, forming a tan crown; perithecia gregarious on a rather superficial stroma or crowded on an erumpent stroma; perithecial wall of 2 regions; perithecia brown, smooth, subglobose to ovoidal; cells of the outer region relatively thick-walled, merging with the cells of the basal stroma, angular to cylindrical, to somewhat hyphal; ascospores ellipsoidal, 1-septate; on bark or herbaceous material of *Brassica* sp. ..... ***Stephanonectria*** Schroers & Samuels (anamorph myrothecium-like with brown conidial masses) (Schroers *et al*., 1999a); one species included, *S. keithii*: ascospores striate, with short striae that are more or less parallel with the long axis, (7.4–)10–11.6–13(–17) × (2.4–)3.2–3.6–4(–5.6) µm; conidial masses ochraceous-brown; Europe, New Zealand, Australia, ?tropical

9 Elements around the ostiole short seta-like, not crown-like, not longer than 30 µm, few-celled, hyphal to tooth-like, wider than the cells of the perithecial wall; apical cells frequently swollen to globose; perithecia pale yellowish, globose to subglobose, without a stroma or seated on hyphae; perithecial wall of 1 region; ascospores ellipsoidal, 1- to 3-septate, smooth, spinulose or striate; hyperparasitic on fungal leaf parasites ..... ***Dimerosporiella*** Speg. (anamorph acremonium-like) (Rossman *et al*., 1999)

10(5) Perithecial wall of 1 region; free-ending elements setose **11**

10 Perithecial wall consisting or 2 regions; free-ending elements hyphal, solitary, short, indistinct or arranged in spike-like to triangular fascicles, sometimes lacking **12**

11 Setae to 200 µm long, scattered on the lateral perithecial wall, with red droplets forming at the tip; perithecia less than 200 µm diam, astromatic, pale orange to greenish, subglobose; asci broadly cylindrical to clavate; ascospores ellipsoidal, 1-celled, smooth; on decaying leaves of *Buxaceae*; temperate ..... ***Pseudonectria*** Seaver (anamorph *Volutella*; *Nectriaceae*) (Rossman *et al*., 1999)

11 Setae to 100 µm long, sparsely scattered on the lateral perithecial wall, lacking apical drops, conspicuously thick-walled; perithecia more than 200 µm diam, without stroma, globose to subglobose, white, yellow, orange to reddish brown; asci broadly clavate, without apical ring; ascospores narrowly ellipsoidal to fusiform, 1- to multiseptate, sometimes disarticulating, smooth; on decaying algae, mosses, or fungicolous; tropical ..... ***Trichonectria*** Kirschst. (anamorph acremonium-like) (Rossman *et al*., 1999)

11 Setae less than 50 µm long, sparsely scattered on the lateral perithecial wall, lacking apical drops, very thick-walled; perithecia less than 200 µm diam, ampulliform, partly immersed in the substratum or superficial, not pigmented, whitish; asci ellipsoidal to cylindrical, with or without an apical ring; ascospores ellipsoidal, 1- or 2-septate; on liverworts and mosses; temperate and tropical ..... ***Bryonectria*** Döbbeler (anamorph unknown) (Döbbeler, 1998)

12 Hyphae arising from the wall solitary or arranged in triangular fascicles, or lacking; perithecia pale yellow to orange, globose to subglobose, apically pinched when dry; without stroma, sometimes seated on or partly embedded in hyphal mat; cells of the outer wall region mainly globose to subglobose, to 30 µm diam, thin-walled, delimited from the hyphae arising from the perithecia; asci clavate, without apical rings; ascospores ellipsoidal, 1- to multiseptate, striate, smooth, or warted; on decaying herbaceous or woody material; tropical to temperate ..... ***Hydropisphaera*** Dumort. (anamorph acremonium-like) (Rossman *et al*., 1999)

12 Hyphae arising in triangular fascicles or solitary; perithecia orange to dark red-orange or dark brown, globose to subglobose; without a stroma; cells of the outer wall region prosenchymatous, possibly continuous with the hyphae arising from the perithecia, of smaller diam, thick-walled; asci clavate; ascospores broadly ellipsoidal, 1-septate, smooth; on dead woody and herbaceous substrata or basidiocarps; temperate ..... ***Lasionectria*** (Sacc.) Cooke (anamorph acremonium-like) (Rossman *et al*., 1999)

13(4) Perithecia without a well-developed basal stroma, seated on the substratum or somewhat immersed in a superficial hyphal mat or a weakly developed stroma, or the outermost cortex of the substratum; perithecia solitary to gregarious **14**

13 Perithecia on a well-developed stroma, which is mostly erumpent through bark of recently dead trees; perithecia crowded in groups of up to 100, rarely solitary **22**

14 Perithecial wall of 1 main region; outermost cells hyphal or epidermoidal or lobed and showing 'pseudopores'; perithecia smooth, pale yellowish to pale orange; ascospores generally 1-septate **15**

14 Perithecial wall of 2 main regions; outermost cells generally globose to angular; perithecia smooth and then light orange to brownish orange or with paler warts; ascospores variously septate **17**

15 Ascospores fusiform, frequently apiculate; hyphal stroma embedding the perithecia or subiculum well-developed ..... ***Hypomyces*** (Fr.) Tul. (*Hypocreaceae*) (anamorphs *Cladobotryum*, *Sepedonium*, *Mycogone*, *Stephanoma*, or acremonium-, verticillium-, papulaspora-like; Rogerson & Samuels, 1989; 1993; 1994)

15 Ascospores not fusiform, rarely apiculate; hyphal stroma only embedding the base of the perithecia; subiculum inconspicuous **16**

16 On basidiocarps of aphyllophoralean fungi; asci cylindrical, ± tube-like; ascospores ellipsoidal, finely warted; perithecia pale orange ..... ***Sphaerostilbella*** (Henn.) Sacc. & D. Sacc. (*Hypocreaceae*) (anamorph *Gliocladium sensu stricto*, including synnematous conidiomata) (Seifert, 1985)

16 On myxomycetes; asci narrowly clavate; ascospores broadly ellipsoidal, ends frequently somewhat truncate, finely warted or smooth; perithecia white, pale yellow, or purple to violet ..... ***Nectriopsis*** *sensu stricto* (anamorph acremonium-like) (Samuels, 1973)

16 Fungicolous on ascomycetes, typically not on basidiomycetes; asci clavate to cylindrical; ascospores of various shape and ornamentation; perithecia white, pale yellow, or pale orange ..... '***Nectriopsis***' (anamorphs diverse; Samuels, 1988a), see also entry 7

17(14) Perithecia smooth **18**

17 Perithecia warted **21**

18 Outer perithecial wall region with intercellular oily orange droplets ..... ***Ochronectria*** Rossman & Samuels (anamorph acremonium–cylindrocarpon-like) (Rossman *et al*., 1999)

18 Perithecial wall without intercellular oily, orange droplets **19**

19 Perithecia solitary, gregarious, or crowded, loosely connected to the substratum, frequently embedded in hyphae, apically pinched when dry, cupulate, smooth or with single or fasciculate hyphae; stroma absent ..... ***Hydropisphaera*** Dumort. (anamorph acremonium-like) (Rossman *et al*., 1999), see also entry 12

19 Perithecia solitary to gregarious, more firmly connected to the substratum, generally not embedded in hyphae, generally pinched laterally or not, smooth or warted, lacking fasciculate hyphae; stroma absent or weakly developed, only erumpent through outer cortex but not penetrating deeper layers of the host plant **20**

20 Stroma superficial, prosenchymatous; perithecia not conspicuously broadly connected to the substratum, yellowish to light orange; main outer wall region of perithecia mostly covered by a single epidermoidal cell layer that merges with the cells of the stroma; interthecial sterile filaments absent; ascospores 1-septate, of variable shape and ornamentation; typically on recently dead leaves, rarely on bark of recently dead trees or lichens ..... ***Bionectria*** subgenus ***Epiphloea*** (anamorph *Clonostachys*, sesquicillium-like) (33–42)

20 Stroma or perithecia erumpent through the outermost layer of the cortex but not penetrating deeper layers of the plant substratum; perithecia broadly connected to the substratum, yellowish or brownish orange; main outer wall region of perithecia not covered by an additional epidermoidal cell layer; interthecial sterile filaments present; ascospores broadly reniform or broadly cymbiform, 1- or multiseptate, striate; on bark of dead trees ..... ***Peethambara*** Subram. & D.J. Bhat (anamorph *Didymostilbe*) (Rossman *et al*., 1999)

21(17) Ascospores with 3–5 septa, oblong ellipsoidal, straight or somewhat curved, smooth to striate; stroma pseudoparenchymatous; perithecia mostly more than 200 µm diam, pale yellow to whit-

ish because of perithecial warts; cells of the warts to 20 µm diam, with unevenly thickened walls; on bark of recently dead trees.....***Albonectria*** Rossman & Samuels (*Nectriaceae*) (anamorph fusarium-like) (Rossman *et al*., 1999)

21 Ascospores 1-septate, sometimes somewhat unequally 2-celled with one end slightly tapering and the other more rounded, ellipsoidal, warted or rough; perithecia less than 200 µm diam, pale yellow to orange; cells of the warts less than 10 µm diam, with unevenly thickened walls; on grasses, ferns, bark, or on superficial or subcortical fungal fruiting structures ....***Bionectria*** subgenus ***Astromata*** (anamorph *Clonostachys*, myrothecium-like) (22–24)

22(13) Perithecial wall of 2 regions; erumpent stroma of prosenchymatous cells; perithecia warted (in one European species smooth); cells of the outer wall region discontinuous with the prosenchymatous cells of the stroma; cells of the warts globose to subglobose, mostly with uniformly thin walls; ascospores 1-septate, conspicuously striate (in one European species smooth); tropical to temperate .....***Bionectria*** subgenus ***Zebrinella*** (anamorph *Clonostachys*)

22 Perithecial wall mostly of 3 regions, with an additional, middle region of intricately arranged hyphae; erumpent stroma of pseudoparenchymatous cells; perithecia warted or smooth; cells of the outer wall region continuous with the pseudoparenchymatous stroma; cells of the warts angular to subglobose, frequently unevenly thick-walled; ascospores generally 1-septate, smooth or warted, rarely with warts arranged in striae **23**

23 Ascospores bean-shaped or straight, ellipsoidal, smooth..... ***Bionectria*** subgenus ***Myronectria*** (25) (anamorph *Clonostachys*, myrothecium-like)

23 Ascospores typically ellipsoidal, generally slightly tapering at the ends, warted ....***Bionectria*** subgenus ***Bionectria*** (anamorph *Clonostachys*, few myrothecium-like) (1–21)

2. Key to selected genera of the *Hypocreales* with penicillate, mononematous and/or synnematous conidiophores, based mainly on characters of the anamorph

1 Conidiomata or conidiophores with differentiated sterile elements such as setae or sterile hyphae that can be straight or curled, branched or unbranched, smooth or verrucose, and sometimes extend conspicuously beyond the hymenium or conidiogenous cells **2**

1 Conidiomata or conidiophores without sterile hyphal elements **14**

2 Conidiophores exclusively mononematous **3**

2 Conidiomata sporodochial to pustulate **7**

2 Conidiomata synnematous **12**

3 Setose extensions ending in a differentiated vesicle; intercalary phialides absent **4**

3 Setae not ending in a differentiated vesicle, generally somewhat tapering towards the tip; intercalary phialides present or absent **5**

4 Setose extensions septate; conidia generally longer than 30 µm ....***Calonectria*** De Not. (*Nectriaceae*) (anamorph *Cylindrocladium* Morgan) (Rossman, 1983; Crous & Wingfield, 1994)

4 Setose extensions non-septate; conidia generally shorter than 25 µm..... .....***Nectricladiella*** Crous & C.L. Schoch (*Nectriaceae*) (anamorph *Cylindrocladiella* Boesew.) (Crous & Wingfield, 1993; Schoch *et al*., 2000)

5 Conidiophores less than 10 µm wide at base; intercalary phialides present, formed below solitary terminal phialides .... ***Bionectria*** subgenus ***Epiphloea*** (anamorph *Clonostachys*, sesquicillium-like) (33–42)

5 Conidiophores more than 10 µm wide at base; intercalary phialides absent.....**6**

6 Conidiophore stipe bearing the penicillus not continuing as a sterile ending main axis; several setae generally arising from the apical part of the conidiophore stipe; setae rather long..... ..... ***Leuconectria*** Rossman, Samuels & Lowen (*Nectriaceae*) (anamorph *Gliocephalotrichum* J.J. Ellis & Hesseltine) (Rossman *et al*., 1993)

6 Conidiophore stipe continuing as a sterile ending, setose main axis; cells forming the penicillus short, arising laterally on the main axis, bearing short cells with irregular clusters of phialides.... ..... ***Chaetopsina*** Rambelli (teleomorph *Cosmospora*; *Nectriaceae*) (Samuels, 1985; Kirk & Sutton, 1985)

7(2) Conidial masses white to orange, not green **8**
7 Conidial masses in light to dark green hues **9**

8 Setae straight, clearly thicker and with thicker walls than the hyphae of the sporodochial subhymenium ..... ***Volutella*** (teleomorphs *Pseudonectria* Seaver and *Cosmospora* Rabenh.; both *Nectriaceae*) (Domsch *et al*., 1980; Rossman *et al*., 1999)
8 Setae undulate, spinose; walls of setae not conspicuously thicker than those of hyphae of the sporodochial subhymenium ..... ***Kutilakesa*** (teleomorph *Nectriella* Nitschke; *Bionectriaceae*) (Alfieri & Samuels, 1979; Rossman *et al*., 1999)

9 Setae arising as sterile apical elongation of the conidiophore main axis; conidiomata loosely pustulate; phialides not forming a compact hymenium ..... ***Trichoderma*** Pers. sect. *Pachybasium* (teleomorph *Hypocrea*; *Hypocreaceae*) (Gams & Bissett, 1998)
9 Setae arising independently or as side branches from lower parts of the conidiophores, not as an apical elongation of the conidiophore main axis; conidiomata generally sporodochial; phialides frequently forming a compact hymenium **10**

10 Sterile elements of curled, branched and/or verrucose marginal hyphae or sometimes relatively thick-walled and wide, straight setae .....***Myrothecium*** and related taxa (Tulloch, 1972)
10 Sterile elements simple, not differentiated, of similar width as the cells of the conidiophore..... **11**

11 Conidiomata cupulate (or simple sporodochial), with a palisade of marginal hyphae/conidiophores extending slightly beyond the hymenium; conidia oval to ellipsoidal, straight, with rather broadly rounded ends, 1-celled, in almost dry chains that can collapse to slimy masses .... ***Bionectria*** subgenus ***Myronectria*** (*Clonostachys*, myrothecium-like) (25)
11 Conidiomata not cupulate; sterile hyphae solitary, extending markedly beyond the hymenium; conidia cylindrical, slightly curved, 1-septate, formed in slimy masses .... **'*Nectria*' *septomyrothecii*** Samuels (?*Bionectriaceae*) (anamorph *Septomyrothecium* Matsush.) (Samuels, 1988b)

12(2) Sterile elements simple, not swollen, hypha-like, protruding beyond the hymenium; hyphae of the synnema stipe smooth, loosely aggregated, not pigmented; conidia 1-celled, smooth, with hyaline, not deeply pigmented walls .....**'*Nectria*'** (?*Peethambara*) ***chlorogloea*** (?*Bionectriaceae*) (anamorph myrothecium-like) (Samuels, 1988b)
12 Sterile elements short, formed at the margin of the synnema stipe, not protruding beyond the hymenium, with frequently swollen, verrucose end-cells; hyphae of synnema stipe densely aggregated, frequently, particularly in the lower part, darkly pigmented; conidia aseptate or multi- to pluriseptate, hyaline or with deeply pigmented walls **13**

13 Conidial masses variously coloured, golden, red, orange, yellow, or dark green; conidia longer than 10 µm, 0–4-septate, smooth or striate; phialides ± clavate with a sometimes inconspicuous cupulate collarette; warted cells on synnema stipe lacking.....***Didymostilbe*** (*Bionectriaceae*) (teleomorph *Peethambara* Subram. & D.J. Bhat) (Seifert, 1985; Rossman *et al*., 1999)
13 Conidial masses orange, pink, red, or dark green; conidia shorter than 7 µm, 1-celled; phialides subulate, lacking a collarette; synnema with globose to ellipsoidal warted cells, at least near top .....***Gracilistilbella*** Seifert (teleomorph *Stilbocrea* Pat.; *Bionectriaceae*) (Rossman *et al*., 1999; Seifert & Samuels, 2000)

14(1) Conidial masses light to dark or almost black-green **15**
14 Conidial masses white, pale yellow or pale orange, or brownish orange..... **22**

15 Conidiophores with complex branching, generally not in well-differentiated stipe and penicillus, effuse or in pustules, with numerous short side branches bearing mostly ampulliform and divergent phialides in whorls or scattered along the hyphae; conidial masses relatively dry, those of

neighbouring side branches generally not coalescing into larger drops ..... ***Trichoderma*** Pers. (somewhat penicillate conidiophores in section *Pachybasium sensu* Bissett (1991) (teleomorph *Hypocrea* Fr.; *Hypocreaceae*) (Samuels *et al*., 1998; Gams & Bissett, 1998)

15 Conidiophores differentiated into stipe and penicillus or entirely sporodochial; conidial masses in watery drops, slimy domes, or imbricate chains that may or may not slime down..... **16**

16 Conidiophores mononematous, monomorphic, penicillate, solitary or in groups arising from the same branching node or hyphae, not in pustules or sporodochia; stipe generally long compared to the height of the penicillus, with or without downward directed sterile branches; conidial masses generally in watery greenish drops, coalescing into larger masses supported by several conidiophores .....***Hypocrea gelatinosa***-group (*Hypocreaceae*) (anamorph gliocladium-like, including *Trichoderma virens* (Miller, Giddens & Foster) von Arx *Gliocladium viride* Matr., *Hypocrea lutea* (Tode : Fr.) Petch (Domsch *et al*., 1980; Gams & Bissett, 1998)

16 Conidiophores of two types (dimorphic), of which one type can form sporodochia or robust synnemata, or entirely sporodochial to synnematous **17**

17 Conidiophores dimorphic, mainly mononematous but sporodochial pustules sometimes present; primary conidiophores verticillium-like or narrowly penicillate, bearing watery hyaline to barely greenish drops of conidia; secondary conidiophores loosely or adpressed penicillate, solitary, aggregated or sporodochial, holding imbricate (green) conidial chains..... .....***Bionectria*** subgenus ***Bionectria*** (anamorph *Clonostachys*) (1–21)

17 Conidiophores primarily sporodochial; mononematous conidiophores, if present, formed in very young sporodochial pustules or not differentiated from the sporodochial conidiophores **18**

18 Conidia almost fusiform with a fan-shaped appendage [***Myrothecium verrucaria*** (Alb. & Schw. : Fr.) Ditm.] or cylindrical without appendage; sporodochia surrounded by sterile, warted hyphae [both characters sometimes difficult to detect in culture] .....***Myrothecium*** spp. (teleomorph unknown; ?*Bionectriaceae*) (Tulloch, 1972)

18 Conidial appendage and warted hyphae absent..... **19**

19 Conidiomata sporodochial to somewhat synnematous, robust, frequently widening in the upper part, funnel-shaped; conidia with deeply pigmented walls (conidial masses olivaceous green), wider than 4 µm, mostly longer than 10 µm, lemon-shaped, slightly curved with one side somewhat flattened, the distal end slightly tapering and somewhat laterally protruding..... .....***Bionectria ralfsii*** (*Clonostachys ralfsii*, subgenus *Bionectria*) (21)

19 Conidiomata flat, sporodochial, not synnema-like, frequently confluent on rich media such as OA; conidia with sub-hyaline walls, less than 10 µm long, of various shapes **20**

20 Phialides cylindrical or minutely widening upwards, narrowing just below the apex, thus appearing apically rounded; conidia ellipsoidal, almost homopolar, hilum median or invisible, rarely slightly displaced..... ***Bionectria*** subgenus ***Myronectria*** (*Clonostachys*, myrothecium-like) (25)

20 Phialides cylindrical to narrowly flask-shaped, slightly narrowing in the upper part but not abruptly below the apex; conidia curved, one side almost flattened, with a more or less laterally displaced hilum or with a slightly laterally protruding base (conidia thus clavate) **21**

21 Branches of conidiophores strongly divergent, ± at right angles; conidia slightly curved with one side slightly flattened; hilum laterally displaced ....***Clonostachys divergens*** (teleomorph unknown; *Bionectria* subgenus *Bionectria*) (20)

21 Conidiophores penicillate, or with phialides arising from single cells borne laterally on hyphae; conidia clavate, the distal end broadly rounded, the proximal end slightly laterally protruding, tapering .....***Bionectria*** subgenus ***Astromata*** (anamorph *Clonostachys*) (22–24)

22(14) Conidia generally 1-septate, cylindrical with rounded ends, hilum invisible; conidiophores solitary to sporodochial; intercalary phialides absent..... ***Gliocladiopsis*** Saksena (teleomorph *Glionectria* Crous & C.L. Schoch; *Nectriaceae*) (Schoch *et al*., 2000)

22 Conidia 0-septate..... **23**
[if conidia 0–1-septate, compare with *Clonostachys setosa* (41) or *Chaetopsina catenulata* Samuels (Samuels, 1985)]

23 Intercalary phialides common, formed below solitary terminal phialides; conidiomata absent **24**
23 Intercalary phialides absent or rarely formed below solitary or whorls of terminal phialides; conidiomata present or absent **26**

24 Conidia fusiform, slightly apiculate, straight; conidial hilum indistinct; conidiophores monomorphic ..... ***Bionectria coronata***, subgenus ***Uniparietina*** (43, 44) (anamorph *Clonostachys*, sesquicillium-like)
24 Conidia ellipsoidal or ovoidal, slightly curved with one somewhat flattened side and with a laterally displaced hilum or straight with an rounded distal end and with or without visible hilum; conidiophores monomorphic or dimorphic **25**

25 Conidia ellipsoidal to ovoid, with rounded ends or with an almost median hilum; conidiophores monomorphic or dimorphic; primary conidiophores if present inconspicuous, acremonium-like, verticillium-like, or narrowly penicillate; secondary conidiophores without setae ..... ***Bionectria*** subgenus ***Zebrinella*** (anamorph *Clonostachys*, sesquicillium-like) (26–32)
25 Conidia slightly curved with one somewhat flattened side and with a laterally displaced hilum or almost straight with a laterally displaced hilum; conidiophores mostly monomorphic; secondary conidiophores in some species setose ..... ***Bionectria*** subgenus ***Epiphloea*** (anamorph *Clonostachys*, sesquicillium-like) (33–42)

26 Conidiation on synnemata, if conidiomata are present, and / or mononematous, mono- or dimorphic conidiophores; conidial masses generally in slimy to watery heads; conidiophore stipes frequently conspicuous because of a base wider than 10 µm and / or a length of more than 300 µm and / or warted cells and / or a reddish-brown pigmentation and / or a relatively thick wall **27**
26 Conidiation on sporodochia, if conidiomata are present, and / or mononematous, mono- or dimorphic conidiophores; conidial masses mostly held in imbricate chains or columns; conidiophore stipe inconspicuous **31**

27 Conidiophore stipe reddish-brown (turning yellow in lactic acid); conidiogenous cells with terminal conidiogenous loci (monophialidic) or with terminal and lateral conidiogenous loci (polyphialidic) ..... ***Chaetopsina*** Rambelli (teleomorph *Cosmospora*; *Nectriaceae*) (Samuels, 1985; Kirk & Sutton, 1985)
27 Conidiophores hyaline or yellow to yellow-orange; conidiogenous loci only terminal (monophialidic) **28**

28 Synnemata present or absent; conidiophore stipes finely warted or smooth; on aphyllophoralean basidiocarps ..... ***Gliocladium*** *sensu stricto* (teleomorphs *Sphaerostilbella* Sacc. (Seifert, 1985) and *Hypocrea* series *Pallidae* (Doi & Yamatoya, 1989) (both *Hypocreaceae*)
28 Synnemata absent; conidiophore stipe smooth; not conspicuously linked to aphyllophoralean substrate **29**

29 Cells of the penicillus clavate, narrowly attached to the supporting cells or the stipe; stipes smooth; on myxomycetes ..... ***Rhopalocladium myxophilum*** (teleomorph *Nectriopsis sporangiicola*; *Bionectriaceae*) (Schroers *et al*., 1999b)
29 Cells of the penicillus cylindrical, rather broadly attached to the supporting cells or the stipe; not linked to myxomycetous substrata **30**

30 Penicillus terverticillate or more highly-verticillate; conidiophore stipe at the base 3.5–4.5 times wider than phialide base; phialidic aperture about 1 µm wide; conidia shorter than 10 µm; conidial masses off-white to tan; cleistothecial ascomata commonly produced in culture ..... ***Roumegueriella rufula*** (*Bionectriaceae*) (anamorph gliocladium-like) (Rossman *et al*., 1999; Schroers *et al*., 1999b)
30 Penicillus less highly branched; conidiophore stipe at the base less than twice the width of the phialide base; phialidic aperture on average wider than 1 µm in width; conidia on average longer than 10 µm; conidial masses yellowish to pale orange; perithecial ascomata sometimes formed in culture ..... ***Bionectria*** subgenus ***Zebrinella*** (anamorph *Clonostachys*, gliocladium-like) (26–32)

31(26) Conidiation entirely sporodochial **32**

31 Conidiation not entirely sporodochial, on mononematous, frequently dimorphic, sometimes sporodochial conidiophores **33**

32 Conidial masses orange-brown, generally collapsing early to slimy masses ..... ***Stephanonectria*** (*Bionectriaceae*) (anamorph sporodochial, Clonostachys-like) (Schroers *et al*., 1999a)

32 Conidial masses pale yellowish to pale orange, at least initially formed in imbricate chains that may or may not collapse to slimy masses ..... ***Bionectria*** subgenus ***Bionectria*** (anamorph Clonostachys-like, sporodochial) (1–21)

33 Conidia ellipsoidal, straight; hilum median, frequently not recognizable; conidiophores monomorphic or indistinctly dimorphic; primary conidiophores adpressed and/or acremonium-like, forming round conidial masses; secondary conidiophores loosely branched, forming imbricate conidial chains or columns or slimy masses..... ***Bionectria*** subgenus ***Zebrinella*** (anamorph *Clonostachys*) (26–32)

33 Conidia ellipsoidal, slightly curved with one side somewhat flattened; hilum laterally displaced (conidia may be straight with the curvature being restricted to the base manifested in a laterally displaced hilum); conidiophores dimorphic; primary conidiophores adpressed or verticillium-like, forming round conidial masses; secondary conidiophores adpressed or loosely to divergently branched forming imbricate conidial chains or columns that may collapse to slimy masses particularly on aggregated conidiophores or sporodochia..... ***Bionectria*** subgenus ***Bionectria*** (anamorph *Clonostachys*) (1–21)

3. Key to species of *Bionectria* / *Clonostachys* based mainly on characters of the ascomata

1 Ascospores conspicuously striate; striae parallel with the long axis, sometimes bifurcated, not composed of warts (Fig. 67 i) ..... ***Bionectria*** (26–32) **2** (anamorph *Clonostachys*, gliocladium-, or sesquicillium-like)

1 Ascospores conspicuously warted **7**

1 Ascospores not as above, smooth, rough or only slightly warted, or with short, inconspicuous striae that can be scattered on the ascospore surface..... **31**

2 75 % of ascospores longer than 20 µm; perithecia generally solitary; conidiophores monomorphic .. ***B. lucifer*** (anamorph *C. lucifer*) (29)
Ascospores (21.4–)27–28.8–30.6(–37) × (6–)8.8–9.4–10(–13.8) µm; conidia (9.8–)12–13.2–14.2(–20) × (5–)6.4–7–7.2(–9) µm.

2 75 % of ascospores shorter than 20 µm; perithecia mostly in crowded groups; conidiophores monomorphic or dimorphic **3**

3 75 % of ascospores longer than 15 µm..... **4**

3 75 % of ascospores shorter than 15 µm..... **5**

4 Anamorph *Clonostachys* sp.; conidiophores more or less monomorphic, gliocladium-like; conidia 0-septate..... ***B. subquaternata*** (anamorph *C. subquaternata*) (28)
Ascospores (10–)15.4–17–18.6(–26) × (3.6–)5.2–6–6.6(–9.6) µm; conidia (5–)9.2–14.8–20.4 (–28.6) × (2.6–)4–6.4–8.6(–12.2) µm.

4 Anamorph *Fusarium* sp., cf. section *Martiella*; conidiophores acremonium-like; conidia partly septate..... ‘***Nectria***’ ***neogrammicospora*** (anamorph *Fusarium* sp.) (Samuels, 1988b)
Ascospores (15.6–)16.6–19.2–21(–26.4) × (4.6–)5.4–6.2–7.2(–8.2) µm.

5 75 % of ascospores less than 4.5 µm wide ... ***B. grammicospora*** (anamorph *C. grammicospora*) (26)
Ascospores (8.2–)10.6–11.6–12.6(–17.6) × (3–)3.8–4.2–4.6(–6.2) µm; conidia (4–)5.4–6–6.8 (–8.8) × (1.8–)2.6–2.8–3(–4) µm.

5 75 % of ascospores wider than 4.5 µm..... **6**

6 75 % of ascospores longer than 12.5 µm; conidiophores more or less monomorphic, gliocladium-like; on bark or ascomycetes; New Zealand, Australia ..... ***B. grammicosporopsis*** (anamorph *C. grammicosporopsis*) (27)
Ascospores (9–)12.6–13.8–15(–18.4) × (3.6–)4.6–5–5.6(–7.4) µm; conidia (4.8–)6.6–7.6–8.4 (–11.6) × (2.2–)3–3.4–3.6(–4.6).

6 75 % of ascospores shorter than 12.5 µm; conidiophores acremonium-like; neotropical ..... '***Nectria***' cf. ***grammicospora*** (anamorph acremonium-like) (Samuels, 1988b)
Ascospores (8.6–)10–11.4–12.6(–14) × (4–)4.8–4.8–5(–6) µm.

7(1) Perithecia in crowded groups of up to 100 or more (solitary perithecia may occur on the same specimen as well), formed on an erumpent stroma mostly on bark of recently dead trees or, rarely, on leaves or herbaceous substrata..... **8**

7 Perithecia solitary, gregarious, formed on a superficial stroma, mostly on decaying leaves or lichens or, bark..... **12a**, **16a, 17b, 25b**

8 75 % of ascospores shorter than 11–11.5 µm..... **9**

8 75 % of ascospores longer than 11–11.5 µm..... **13**

9 Perithecia at least with small warts, rather pale yellowish; walls of cells of the warts uniformly thin; asci frequently without an apical ring..... ***B. sporodochialis*** (anamorph *C. sporodochialis*) (10)
Ascospores (7.8–)9.6–10.4–11(–13) × (2.6–)3.2–3.6–3.8(–5) µm; conidia (3.2–)4.4–4.8–5.4 (–6.8) × (1.6–)2.0–2.2–2.2(–2.6) µm.

9 Perithecia smooth to rough, not warted, pale yellow or pale to light orange; outermost cells with uniformly or, if perithecia are rough, with unevenly thickened walls; asci with an apical ring . **10**

10 75 % of ascospores shorter than 9–9.5 µm..... ***B. pseudochroleuca*** (anamorph *C. pseudochroleuca*) (17)
Ascospores (6–)8.4–8.8–9.4(–11) × (2.2–)2.8–3.2–3.4(–4.4) µm; conidia (3.2–)4–4.4–4.6(–6.4) × (1.2–)2.2–2.2–2.4(–3) µm.

10 75 % of ascospores longer than 9–9.5 µm..... **11**

11 Perithecia typically rough; outermost cells of the perithecial wall frequently with unevenly thickened walls ..... ***B. ochroleuca*** (anamorph *C. rosea*) (5)
Ascospores (7.4–)9.4–10–10.8(–14.4) × (2.2–)3–3.4–3.6(–4.8) µm; conidia (4.2–)4.8–5.2–5.6 (–6.6) × (2–)2.4–2.8–3(–3.4) µm (those from primary conidiophores to 15.4 µm long).

11 Perithecia typically smooth; outermost cells of the perithecial wall with unevenly thickened walls... **12**

12 Perithecial wall of 2 regions; middle, hyphal region lacking; intercalary phialides present, formed below solitary terminal phialides; neotropical..... ***B. sesquicillii*** (anamorph *C. sesquicillii*) (38)
Ascospores (8.2–)10–10.8–11.4(–14.4) × (2.2–)2.8–3.2–3.2(–4.4) µm; conidia (4.2–)5–5.8–6 (–9.6) × (1.6–)2.2–2.2–2.4(–3) µm.

12 Perithecial wall of 3 regions; middle, hyphal region present; intercalary phialides lacking or rare, mostly formed below whorls of terminal phialides; known mainly from temperate regions such as Eastern U.S.A., France, Japan, possibly rare in tropical regions..... ***B. compactiuscula*** (anamorph *C. compactiuscula*) (13)
Ascospores (6.2–)9–9.8–10.4(–13.4) × (2.2–)2.8–3.2–3.4(–4.4) µm; conidia (3.9–)5.4–6.6–7.5(–12.4) × (1.5–)1.9–2.2–2.5(–3.2) µm.

13(8) 75 % of ascospores longer than 20 µm..... ***B. tonduzii*** / ***B. apocyni*** (anamorph *C. macrospora*) (1, 2)
Ascospores (16–)20.6–22.6–24.6(–32) × (4.6–)6–6.8–7.6(–9.4) µm; conidia (6.0–)11.2–13–15(–20.2) × (3.2–)4.6–5–5.4(–7) µm.

13 75 % of ascospores shorter than 20 µm..... **14**

14 75 % of ascospores wider than 4.5 µm..... **15**

14 75 % of ascospores less than 4.5 µm wide..... **21**

15 Perithecia smooth..... **16**

15 Perithecia warted..... **19**

16 Known from *Rhopalostylis sapida* (New Zealand); conidiophores dimorphic; primary conidiophores with divergent phialides .....***B. verrucispora*** (anamorph *Clonostachys verrucispora*) (12)
Ascospores (12.2–)14–15.6–17(–19.2) × (4.4–)5.4–5.8–6.2(–7) µm; conidia (5.6–)7.4–8.4–9.2(–15.6) × (2.2–)3–3.2–3.6(–4.4) µm.

16 On bark of recently dead trees, lichens, rarely decaying leaves; conidiophores dimorphic and then with adpressed primary conidiophores, or monomorphic and then frequently forming intercalary phialides below solitary terminal phialides **17**

17 Ascospores shorter than 16 µm; conidiophores dimorphic; primary conidiophores narrowly adpressed; New Zealand and neotropical ..... ***B. aureofulvella*** (anamorph *C. aureofulvella*) (16)
Ascospores (9.6–)12.6–13.2–13.8(–16) × (3.4–)4.6–5–5.6(–7.2) µm; conidia (3.6–)4.8–5.8–7(–9) × (1.8–)2.4–2.8–3.2(–3.8) µm.

17 75 % of ascospores longer than 16 µm; conidiophores monomorphic; intercalary phialides formed frequently, below solitary terminal phialides **18**

18 Warts of ascospores inconspicuous, almost rod-shaped, intricately arranged; ascospores somewhat curved, with rather broadly rounded ends .....***B. impariphialis*** (anamorph *C. impariphialis*) (34)
Ascospores (15.2–)17.8–18.6–19(–23) × (4.4–)5.6–6–6.4(–7.2) µm; conidia (5.6–)7.6–9.6–10(–12) × (3–)3.4–3.6–3.8(–4.6) µm.

18 Ascospores coarsely warted or smooth, tapering towards the ends .....
.....***B. parviphialis*** (anamorph *C. pseudosetosa*) (35)
Ascospores (13.2–)16.2–18.8–21.6(–24.8) × (4.4–)5.6–6.8–8(–10) µm; conidia (8–)10–11.2–12.4(–15.2) × (3–)3.4–3.8–4(–4.6) µm (natural substratum); (8.7–)11.2–15.2(–17.5) × (3.3–)3.5–4.5(–4.7) µm (in culture).

19(15) Cells of perithecial warts with uniformly thin walls; New Zealand .....
..... ***B. zelandiaenovae*** (anamorph *C. zelandiaenovae*) (11)
Ascospores (11.6–)14.6–15.8–16.8(–21.4) × (3.8–)5–5.4–5.8(–7.4) µm; conidia (4–)5.2–6–6.4(–13.2) × (2.4–)2.8–3–3.2(–4.2) µm.

19 Cells of perithecial warts with unevenly thickened walls [compare also with *B. byssicola* that can have ascospores wider than 4.5 µm] **20**

20 Perithecial walls of three regions; middle, hyphal region present; conidia typically longer than 10 µm; Japan and ?neotropical .....***B. oblongispora*** (anamorph *C. oblongispora*) (3)
Ascospores (16–)16.8–17.6–18.2(–20) × (4.2–)4.8–5–5.4(–5.8) µm; conidia (9–)12.6–13.6–14(–19.8) × (2.6–)3.2–3.6–3.8(–4.2) µm.

20 Perithecial walls of two regions; middle, hyphal region lacking; conidia mostly shorter than 10 µm; Japan .....***B. capitata*** (*C. capitata*) (8)
Ascospores (11.6–)13.8–14.8–15.6(–18.8) × (3.6–)4.2–4.8–5(–5.8) µm; conidia (4.6–)6–6.8–7.2(–12.4) × (2.2–)2.8–3.2–3.4(–4.2) µm.

21(14) Perithecia smooth, brown or brownish orange **22**

21 Perithecia smooth or warted, pale yellow, pale to light orange, or brownish orange..... **23**

22 Ascospore warts arranged in striae; conidiation on dimorphic, mononematous conidiophores and sporodochia; Indonesia, Japan .....***B. pseudostriata*** (anamorph *C. pseudostriata*) (18)
Ascospores (9–)10.6–12.4–14.4(–17.2) × (3–)3.6–4.2–4.6(–5.8) µm; conidia (3.6–)5–5.6–6.2(–8) × (2–)2.6–3–3.2(–3.8) µm.

22 Ascospores warts irregularly scattered; conidiation only on sporodochia; common in neotropical regions ..... ***B. samuelsii*** (anamorph *C. samuelsii*) (19)
Ascospores (7.8–)10.4–11.4–12.2(–15.4) × (2.8–)3.6–3.8–4(–5.6) µm; conidia (4.4–)5.8–6.6–7(–11.6) × (2.2–)2.6–2.8–3(–3.8) µm.

23 Perithecia warted **24**

23 Perithecia smooth or rough, inconspicuously warted..... **27**

24 Cells of perithecial warts uniformly thin-walled; perithecia rather pale yellowish to pale orange; asci frequently without an apical ring.....***B. sporodochialis*** (anamorph *C. sporodochialis*) (10)
Ascospores (7.8–)9.6–10.4–11(–13) × (2.6–)3.2–3.6–3.8(–5) µm; conidia (3.2–)4.4–4.8–5.4(–6.8) × (1.6–)2.0–2.2–2.2(–2.6) µm.

24 Cells of perithecial warts unevenly thick walled; perithecia mostly pale to light orange or whitish because of the colour of the warts; asci with an apical ring **25**

25 Perithecia typically in crowded groups on an erumpent stroma, rarely solitary; ascospores uniformly 2-celled; perithecial wall of three regions, hyphal region present; sporodochia forming pale orange or whitish conidial masses frequently close to, independently formed of the perithecia; on woody substrata, generally not on grasses or ferns; conidial masses whitish to pale orange ..... ***B. byssicola*** (anamorph *C. byssicola*) (6)
Ascospores (8.4–)11.2–12.4–13.4(–19.8) × (2.6–)3.8–4.2–4.6(–7.4) µm; conidia (3.2–)4.4–5.2–5.8(–10.8) × (1.8–)2.4–2.6–2.8(–4) µm.

25 Perithecia more or less directly on the substratum, without a stroma; ascospores somewhat unevenly 2-celled, with one end slightly tapering, the other slightly more rounded; perithecial wall of two regions, hyphal region lacking; sporodochia forming green conidial masses frequently next to the perithecia; on fungal substrata, often on grasses or ferns; conidial masses green **26**

26 75 % of ascospores shorter than 12 µm; conidiophores of sporodochia penicillate .... ***B. epichloë*** (anamorph *C. epichloë*) (22)
Ascospores (7.2–)9–9.8–10.8(–13) × (2.4–)3–3.4–4(–4.4) µm; conidia (4.8–)6–6.6–7(–9.6) × (1.6–)2.2–2.6–2.8(–3.6) µm.

26 75 % of ascospores longer than 12 µm; conidiophores of sporodochia irregularly penicillate or with phialides scattered laterally on hyphal or almost isodiametrical cells .... ***B. parva*** (anamorph ?*C. miodochialis*) (23)
Ascospores (10–)12.2–13–13.4(–15.8) × (2.8–)3.4–3.8–4(–4.6) µm; conidia (4.6–)5.4–5.6–6(–6.6) × (1.8–)2.2–2.4–2.6(–3) µm.

27(23) Outermost cells of perithecia with unevenly thickened walls; conidiophores dimorphic; primary conidiophores verticillium-like, secondary conidiophores adpressed .... ***B. ochroleuca*** (anamorph *C. rosea*) (5)
Ascospores (7.4–)9.4–10–10.8(–14.4) × (2.2–)3–3.4–3.6(–4.8) µm; conidia (4.2–)4.8–5.2–5.6(–6.6) × (2–)2.4–2.8–3(–3.4) µm (those from primary conidiophores to 15.4 µm long).

27 Outermost cells of perithecia with uniformly thin walls; conidiophores showing other branching patterns **28**

28 Perithecial wall of two regions; hyphal, middle region lacking; intercalary phialides frequently formed below solitary phialides **29**

28 Perithecial wall of three regions; hyphal, middle region present; intercalary phialides rarely formed, mostly absent **30**

29 Known from bark or leaves of *Buxus* and then with smooth ascospores ?or from parts of *Solanum tuberosum*; temperate, Europe ..... ***B. levigata*** (anamorph *C. levigata*) (30)
Ascospores (9.8–)11.2–11.8–12.4(–15.6) × (2.6–)3.2–3.4–3.8(–4) µm; conidia (4–)5.6–6–6.4(–7.6) × (2.0–)2.4–2.6–2.6(–3) µm.

29 Known from bark of recently dead trees or decaying leaves; neotropical..... ..... ***B. sesquicillii*** (anamorph *C. sesquicillii*) (38)
Ascospores (8.2–)10–10.8–11.4(–14.4) × (2.2–)2.8–3.2–3.2(–4.4) µm; conidia (4.2–)5–5.8–6(–9.6) × (1.6–)2.2–2.2–2.4(–3) µm.

30 Cells of the outer perithecial wall surrounding the ostiole cylindrical, arranged vertically; perithecia common, tropical; conidiation entirely from sporodochia; sporodochia frequently close to perithecia, remnants of sporodochia frequently covering parts of perithecial clusters; phialides narrowing below the tip, appearing apically rounded; conidia ellipsoidal, ± straight, without a visible or a very slightly laterally displaced hilum ..... ***B. samuelsii*** (anamorph *C. samuelsii*) (19)
Ascospores (7.8–)10.4–11.4–12.2(–15.4) × (2.8–)3.6–3.8–4(–5.6) µm; conidia (4.4–)5.8–6.6–7(–11.6) × (2.2–)2.6–2.8–3(–3.8) µm.

30 Cells of the outer perithecial wall surrounding the ostiole angular; perithecia not very common, temperate and tropical; conidiation from sporodochia as well as dimorphic, mononematous conidiophores; phialides apically straight, truncate; conidia ellipsoidal, slightly curved, with one somewhat flattened side and a laterally displaced hilum ..... ***B. solani*** (anamorph *C. solani*) (15)

31(1) Ascospores mostly longer than 22 µm, frequently slightly curved with rounded ends, bean-shaped; perithecia crowded, formed on an erumpent stroma ..... ***Bionectria pityrodes*** (anamorph *C. pityrodes*) (25)
Ascospores (15.4–)24.2–26.8–29(–39.6) × (6.4–)8.2–9.2–10.2(–13.2) µm; conidia (4.8–)5.8–6.6–7.2(–9.0) × (2.4–)2.8–3–3.4(–4) µm.

31 75 % of ascospores shorter than 22 µm, not bean-shaped; perithecia solitary, gregarious, or in small groups; perithecial stroma prosenchymatous, superficial, rarely weakly erumpent..... **32**

32 Ascospores typically longer than 15 µm **33**

32 Ascospores typically shorter than 15 µm **38**

33 Perithecia at least with small warts..... **34**

33 Perithecia smooth **35**

34 Perithecia at least in dry condition appearing wider than high, frequently with somewhat sunken apex, formed on a weakly erumpent or ± superficial stroma; frequently associated with a sporodochial anamorph forming green conidial masses; on bark of various recently dead trees; Europe, New Zealand, SW Australia..... ***B. ralfsii*** (anamorph *C. ralfsii*) (21)
Ascospores (14.6–)17.6–18.6–19.4(–22.8) × (5.4–)6–6.6–7.2(–8) µm; conidia (7.4–)11.6–12.6–13.6(–17.8) × (4.8–)6.4–7–7.6(–11) µm.

34 Perithecia almost globose; formed on a well-developed, erumpent stroma; anamorph forming hyaline conidia in white to orange masses; on bark of *Sophora microphylla* (kowhai); only known for New Zealand..... ***B. kowhaii*** (anamorph *C. kowhaii*) (4)
Ascospores (14.6–)16.6–18.2–19.6(–23.2) × (5–)5.8–6.4–7(–8.4) µm; conidia (4.4–)7.6–10.6–13.2(–18.2) × (2.8–)3.4–4–4.6(–5.8) µm.

35 L/W of ascospores typically more than 4; ascospores typically less than 4 µm wide..... **36**

35 L/W of ascospores typically less than 4; ascospores typically wider than 4 µm..... **37**

36 Cells below the surface of the perithecial wall typically less than 10 µm in greatest dimension ..... ***B. lasiacidis*** (anamorph *C. lasiacidis*) (37)
Ascospores (13.6–)17–18–19(–21.4) × (2.6–)3.4–3.6–3.8(–4.4) µm; conidia (5.6–)6.4–7–7.6(–8.2) × (1.8–)2.2–2.4–2.8(–3.2) µm.

36 Cells below the surface of the perithecial wall typically more than 10 µm in greatest dimension..... ***B. tornata*** (anamorph *C. asymmetrica*) (36)
Ascospores (9–)10.8–12.8–14.2(–20.8) × (2–)2.4–2.6–3(–4) µm; conidia (8–)10.2–12–13(–19.2) × (2.4–)2.8–3.0–3.2(–3.8) µm (in culture).

37 Warts of ascospores inconspicuous, almost rod-shaped, intricately arranged; ascospores somewhat curved, with rather broadly rounded ends ..... ***B. impariphialis*** (anamorph *C. impariphialis*) (34)
Ascospores (15.2–)17.8–18.6–19(–23) × (4.4–)5.6–6–6.4(–7.2) µm; conidia (5.6–)7.6–9.6–10(–12) × (3–)3.4–3.6–3.8(–4.6) µm.

37 Ascospores coarsely warted or smooth, tapering towards the ends..... ***B. parviphialis*** (anamorph *C. pseudosetosa*) (35)
Ascospores (13.2–)16.2–18.8–21.6(–24.8) × (4.4–)5.6–6.8–8(–10) µm; conidia (8–)10–11.2–12.4(–15.2) × (3–)3.4–3.8–4(–4.6) µm (natural substratum); (8.7–)11.2–15.2(–17.5) × (3.3–)3.5–4.5(–4.7) µm (in culture).

38(32) Ascospores 1-septate, ellipsoidal; perithecial wall of 1 or 2 main regions; not known from *Buxus*, at least not restricted to *Buxus*..... **39**

38 Ascospores 0-septate, somewhat cymbiform; perithecial wall of 1 region; only on *Buxus*..... ***B. coronata*** (anamorph *C. buxi*) (43)
Ascospores (8.8–)10.4–11.4–12(–14.8) × (2.6–)3–3.2–3.4(–4); conidia (5.4–)6.4–6.8–7(–8) × (1.6–)1.8–2–2.4(–2.6) µm.

39 Perithecial wall consisting 1 region; Indonesia ..... ***B. aurantia*** (44)
Ascospores 8–11 × 2.2–3.6 µm.

39 Perithecial wall consisting 2 main regions **40**

40 L/W of ascospores typically more than 4 ..... ***B. tornata*** (anamorph *C. asymmetrica*) (36)
Ascospores (9–)10.8–12.8–14.2(–20.8) × (2–)2.4–2.6–3(–4) µm; conidia (8–)10.2–12–13 (–19.2) × (2.4–)2.8–3.0–3.2(–3.8) µm (culture).

40 L/W of ascospores typically more than 4 ..... **41**

41 Perithecia with a hump-like thickening around the ostiole; U.S.A., Florida .....
..... ***B. gibberosa*** (anamorph *C.* cf. *setosa*) (42)
Ascospores (9–)11–12–13(–15) × (2–)3–3.5–4(–5.5) µm; conidia (7.6–)10–10.8–11.4(–14.4) × (1.8–)2.2–2.4–2.6(–3) µm (teleomorph–anamorph connection not proven).

41 Perithecia without a hump-like thickening around the ostiole; neotropical **42**

42 Perithecia brown; ascospores smooth or inconspicuously striate .....
..... ***B. setosa*** (anamorph *C. setosa*) (41)
Ascospores (8.8–)10.2(–13) × (2.4–)3(–3.8) µm; conidia (8.6–)10.2–12–13.4(–19.2) × (2–)2.6–2.6–2.6(–3.2) µm.

42 Perithecia light orange; ascospores finely striate, with short striae that are more or less parallel to the long axis..... ***B. rossmaniae*** (*C. rossmaniae*) (33)
Ascospores (7.4–)10–10.8–11.6(–13.8) × (2.2–)3–3.2–3.6(–4.6) µm; conidia (4.2–)4.6–5–5.4 (–6.6) × (2–)2.2–2.4–2.4(–2.8) µm.

4. Key to species of *Bionectria* / *Clonostachys* and similar taxa, based mainly on characters of the anamorph from pure culture

1 Conidial masses green..... **2**

1 Conidial masses not green, but whitish, yellowish, pale orange to brownish orange, rarely brown .. **9**

2 Conidiation on pustules that typically develop into distinct or confluent sporodochia; mononematous conidiophores absent **3**

2 Conidiation on mononematous, dimorphic, rarely monomorphic conidiophores; sporodochial pustules or conidiomata in addition to the mononematous conidiophores present or absent **7**

3 Phialides cylindrical or minutely widening upwards, subapically narrowing, apex therefore appearing somewhat rounded; conidia ellipsoidal to ovoidal, ends ± broadly rounded, in imbricate chains that may collapse to slimy masses; hilum hardly visible, ± median; conidiation in pustules or, with time, in well-developed, sometimes cupulate sporodochia; conidiophores of the sporodochia frequently joined by anastomoses or small bridges.....
..... ***B. pityrodes*** (anamorph *C. pityrodes*) (25)
Conidia (4.8–)5.8–6.6–7.2(–9.0) × (2.4–)2.8–3–3.4(–4) µm.

3 Phialides narrowly flask-shaped, cylindrical, rarely subulate; apex truncate, not narrowing subapically; conidia generally slightly curved, with one side more flattened, slightly clavate, or lemon-shaped; hilum laterally displaced or sometimes somewhat protruding; sporodochia flat dome-shaped, not cupulate; anastomoses rare or absent **4**

4 Conidia wider than 4 µm, at least 75 % of conidia longer than 10 µm, with deeply pigmented walls, somewhat lemon-shaped, with a tapering, somewhat protruding distal end; hilum almost median ..... ***B. ralfsii*** (anamorph *C. ralfsii*) (21)
Conidia (7.4–)11.6–12.6–13.6(–17.8) × (4.8–)6.4–7–7.6(–11) µm.

4 Conidia less than 4 µm wide, hyaline or greenish hyaline, not lemon-shaped..... **5**

5 Branches of conidiophores and phialides, particularly in young sporodochial pustules, strongly divergent, almost rectangular; young pustules with separate conidial chains formed by each phialide; conidia of confluent sporodochia more and more columnar and collapsing to slimy masses; conidia ellipsoidal; with flat hilum..... ***C. divergens*** (20)
Conidia (4.8–)5.8–6.2–6.4(–7.4) × (2.6–)3.2–3.2–3.2(–3.8) µm.

5 Branches of conidiophores and phialides less strongly divergent or adpressed; conidia formed in columns or packed chains that may collapse to slimy masses; conidia slightly clavate because of a slightly protruding proximal end..... **6**

6 Sporodochial conidiophores penicillate, generally only two branches arising from a metula..... ..... ***B. epichloë*** (anamorph *C. epichloë*) (22)
Conidia (4.8–)6–6.6–7(–9.6) × (1.6–)2.2–2.6–2.8(–3.6) µm.

6 Sporodochial conidiophores rarely penicillate; phialides typically seated directly on aggregates of angular cells or mostly paired phialides seated on short supporting cells that are scattered laterally on hyphae ..... ***C. miodochialis*** (teleomorph ?*B. parva*) (24)
Conidia (5.2–)5.8–6.6–7.2(–8) × (1.8–)2.6–2.8–3(–3.4) µm.

7(2) Conidiophores appearing monomorphic, verticillium-like; conidial masses hyaline or obscurely greenish, formed in small watery heads on each of the divergent phialides; secondary conidiophores rare or lacking..... ***C. rhizophaga*** (7)

7 Conidiophores consistently dimorphic; conidia of primary conidiophores formed in watery heads, those of secondary in greenish imbricate columns..... **8**

8 Primary conidiophores verticillium-like; branches and / or phialides divergent; conidia in small heads formed at the tip of each of the phialides; secondary conidiophores generally adpressed, forming narrow and long imbricate chains of conidia; sporodochia generally absent in culture ... . ***C. rosea*** f. ***catenulata*** (5)
Conidia (4–)4.8–5–5.4(–6) × (2.2–)2.4–2.6–2.8(–3) µm.

8 Primary conidiophores narrowly penicillate; branches and phialides adpressed; conidia formed in larger heads on the penicillus; branches of the secondary conidiophores more divergent, typically forming short or long imbricate chains of conidia; sporodochia of secondary conidiophores frequently formed in culture..... ***C. solani*** f. ***nigrovirens*** (15)
Conidia of secondary conidiophores (3.4–)4.2–4.6–4.8(–6.4) × (2.2–)2.6–2.8–3(–3.8) µm.

9(1) Conidiation entirely sporodochial; sporodochia flat, robust, or sometimes synnema-like in older colonies, without setae; intercalary phialides absent **10**

9 Conidiation not entirely sporodochial, on mononematous, frequently dimorphic, sometimes sporodochial conidiophores; setae rarely formed in some sesquicillium-like anamorphs; intercalary phialides present or absent **12**

10 Conidia slightly curved, with a laterally displaced hilum; phialides with truncate apex, mostly (75 %) longer than 15 µm; conidial masses pale to light orange; neotropical regions..... ..... ***B. sporodochialis*** (anamorph *C. sporodochialis*) (10)
Conidia (3.2–)4.4–4.8–5.4(–6.8) × (1.6–)2.0–2.2–2.2(–2.6) µm.

10 Conidia ellipsoidal, straight; hilum hardly laterally displaced, median or invisible; phialides narrowing below the apex that appears somewhat rounded, mostly (75 %) shorter than 15 µm; conidial masses frequently with a brownish shade **11**

11 75 % of conidia longer than 6 µm; branches of conidiophores frequently widening apically; conidial masses pale orange to brownish orange; only known from ascospore isolations; tropical..... ..... ***B. samuelsii*** (anamorph *C. samuelsii*) (19)
Conidia (4.4–)5.8–6.6–7(–11.6) × (2.2–)2.6–2.8–3(–3.8) µm.

11 75 % of conidia shorter than 6 µm; branches of conidiophores cylindrical, not widening apically; conidial masses ochraceous-brown to deep brown; conidial isolates known from soil; teleomorph known from dead stipes of *Brassica* sp. and bark of dead trees; Europe, New Zealand, and ?tropical ..... ***Stephanonectria keithii*** (anamorph myrothecium-like with brown conidial masses) (Schroers *et al*., 1999a)
Conidia (3.4–)4.8–5.4–6(–7.8) × (1.8–)2.2–2.4–2.6(–3.2) µm.

12 Intercalary phialides formed regularly below solitary terminal phialides (of secondary conidiophores if conidiophores dimorphic); conidiophores monomorphic or, rarely, dimorphic; setae present or absent; sporodochia absent **13**

12 Intercalary phialides absent or rare, sometimes formed below whorls of terminal phialides, rarely below solitary terminal phialides; conidiophores mono- or dimorphic; setae absent; sporodochia absent or present..... **24**

13 L/W of conidia more than 4; conidia mostly 1-celled, rarely 1-septate..... **14**

13 L/W of conidia less than 4; conidia always 1-celled..... **15**

14 Conidia slightly tapering at both ends, typically slightly curved or with one flattened side; setae sometimes arising from conidiophores as branches .. ***B. tornata*** (anamorph *C. asymmetrica*) (36)
Conidia (8–)10.2–12–13(–19.2) × (2.4–)2.8–3.0–3.2(–3.8) µm.

14 Conidia not tapering, with a rounded distal end, straight, cylindrical, or with curvature restricted to the proximal end; setae generally arising from conidiophores as branches..... ..... ***B. setosa*** or ***B. gibberosa*** [anamorph *C. setosa* (41) or *C.* cf. *setosa* (42)]
Conidia (8.6–)10.2–12–13.4(–19.2) × (2–)2.6–2.6–2.6(–3.2) µm (*B. setosa*).

15 75 % of conidia more than 3.5 wide **16**

15 75 % of conidia less than 3.5 wide **18**

16 75 % of conidia shorter than 7.5 µm; conidia broadly ellipsoidal, with broadly rounded ends, straight, with ± invisible hilum; conidiophores dimorphic; early formed conidiophores of few divergent phialides borne on short stipes, without intercalary phialides ..... ***C. chlorina*** (32)
Conidia (6.2–)7–7.2–7.4(–8.8) × (3.2–)3.6–4–4.2(–4.4) µm**.**

16 75 % of conidia longer than 7.5 µm; conidia either slightly curved or with one slightly flattened side, or, if straight, with a visible hilum; conidiophores monomorphic or obscurely dimorphic **17**

17 75 % of conidia shorter than 10 µm; intercalary phialides and terminal phialides typically 10–15 µm long; setae absent ..... ***B. impariphialis*** [anamorph *C. impariphiale* (34) (Samuels, 1989)]
Conidia (5.6–)7.6–9.6–10(–12) × (3–)3.4–3.6–3.8(–4.6) µm.

17 75 % of conidia longer than 10 µm; intercalary phialides 5–10 µm long; terminal phialides 6.5–12 µm long; setae sometimes arising from conidiophores as branches .... ***B. parviphialis*** (anamorph *C. pseudosetosa*) (35)
Conidia (8.7–)11.2–15.2(–17.5) × (3.3–)3.5–4.5(–4.7) µm.

18 Branches of penicillus divergent..... **19**

18 Branches of penicillus adpressed (primary branches can be divergent if the terminal branches form dense whorls)..... **20**

19 Conidia longer than 5.5 µm; neotropical ..... ***B. lasiacidis*** (anamorph *C. lasiacidis*) (37)
Conidia (5.6–)6.4–7–7.6(–8.2) × (1.8–)2.2–2.4–2.8(–3.2) µm.

19 Conidia generally shorter than 5.5 µm; temperate ..... ***C. candelabrum*** (39)
Conidia 3–5.5 × 1.8–3.4 µm.

20 Conidia without visible hilum, straight, both ends slightly tapering, ellipsoidal to oblong-ellipsoidal to cymbiform; known only from *Buxus* ..... ***B. coronata*** (anamorph *C. coronata*) (43)
Conidia (5.4–)6.4–6.8–7(–8) × (1.6–)1.8–2–2.4(–2.6) µm.

20 Conidia with a visible, generally laterally displaced hilum, mostly slightly curved or with one somewhat flattened side; distal end rounded or somewhat tapering; not linked to *Buxus* **21**

21 Setae frequently arising from submerged hyphae or as branches from conidiophores .... ***C. phyllophila*** (40)
Conidia (5.4–)5.8–6.4–7(–8.8) × (2.2–)2.6–2.8–3(–3.2) µm.

21 Setae absent **22**

22 Conidia typically longer than 10 µm ..... ***B. tornata*** (*C. asymmetrica*) (36)
Conidia (8–)10.2–12–13(–19.2) × (2.4–)2.8–3.0–3.2(–3.8) µm.

22 Conidia typically shorter than 10 µm **23**

23 75 % of conidia with a L/W of 2.2–2.7(–4.2); verticillium-like conidiophores rare; secondary conidiophores narrowly penicillate, penicillus to 40 µm diam.... ***B. sesquicillii*** (*C. sesquicillii*) (38)
Conidia (4.2–)5–5.8–6(–9.6) × (1.6–)2.2–2.2–2.4(–3) µm.

23 75 % of conidia with a L/W of 2–2.3(–3.3); verticillium-like synanamorph absent; penicillus mostly 40–60 µm diam ..... ***B. rossmaniae*** (*C. rossmaniae*) (33)
Conidia (4.2–)4.6–5–5.4(–6.6) × (2–)2.2–2.4–2.4(–2.8) µm.

24(12) 75 % of conidia longer than 7.5–8 µm, on average exceeding than 10 µm **25**

24 75 % of conidia shorter than 8 µm..... **29**

25 Conidia straight, ovoidal to ellipsoidal; distal end typically broadly rounded; proximal end broadly rounded, without visible hilum or with a ± median hilum; conidiophores monomorphic, penicillate, adpressed, sparsely branched; conidiomata absent; colonies typically deep yellow..... **26**

25 Conidia slightly curved, with one side somewhat flattened and with a laterally displaced hilum or oblong-ellipsoidal to obclavate with an obscurely visible hilum; proximal end rounded or slightly tapering; conidiophores dimorphic; primary conidiophores verticillium-like, rarely formed; secondary conidiophores loosely branched, frequently aggregated; conidiomata present at least on the natural substratum, rare in culture; colonies not pigmented or pale yellowish to pale orange..... **27**

26 Metulae generally longer than 20 µm; 75 % of phialides longer than 15 µm; perithecia sometimes present in culture, solitary, light orange..... ***B. subquaternata*** (anamorph *C. subquaternata*) (28)
Conidia (5–)9.2–14.8–20.4(–28.6) × (2.6–)4–6.4–8.6(–12.2) µm.

26 Metulae generally shorter than 20 µm; 75 % of phialides shorter than 18 µm; perithecia not observed in culture ..... ***B. lucifer*** (*Clonostachys lucifer*, gliocladium-like) (29)
Conidia (9.8–)12–13.2–14.2(–20) × (5–)6.4–7–7.2(–9) µm.

27 Colonies slow-growing, less than 10 mm diam; conidia of variable shape, frequently widest in the lower part (obclavate) or oblong ellipsoidal, hilum frequently median; New Zealand.....
..... ***B. kowhaii*** (anamorph *C. kowhaii*) (4)
Conidia (4.4–)7.6–10.6–13.2(–18.2) × (2.8–)3.4–4–4.6(–5.8) µm.

27 Colonies growing faster, more than 20 mm diam; conidia typically slightly curved with one side flattened and a laterally displaced hilum **28**

28 Conidia on average narrower than 4 µm; distal end ± rounded.....
..... ***B. oblongispora*** (anamorph *C. oblongispora*) (3)
Conidia (9–)12.6–13.6–14(–19.8) × (2.6–)3.2–3.6–3.8(–4.2) µm.

28 Conidia on average wider than 4 µm; distal end tapering.....
..... ***B. apocyni*** (anamorph *C. macrospora*) (2)
Conidia (6.0–)11.2–13–15(–20.2) × (3.2–)4.6–5–5.4(–7) µm.

28 Conidial shape indistinguishable from *B. apocyni*; conidia slightly smaller, (6.8–)8–9.8–11.6 (–15.4) × (2.6–)3.2–3.4–3.8(–5.8) µm, only known from the natural substratum associated with perithecia; conidiophores not observed ..... ***B. tonduzii*** (anamorph *C.* ?*macrospora*) (1)

29(24) Conidia straight, ovoidal to ellipsoidal; distal end rounded; hilum not or obscurely visible, median, or very slightly laterally displaced; conidiophores mono- or dimorphic, both types can be obscure or lacking; intercalary phialides present or absent; conidiomata absent **30**

29 Conidia slightly curved, with one somewhat flattened side; distal end slightly tapering or rounded; hilum typically laterally displaced; conidiophores typically dimorphic, although either the primary or the secondary can be obscure or sometimes lacking; intercalary phialides rare or absent, generally not formed below solitary terminal phialides; conidiomata absent or present **36**

30 Primary conidiophores verticillium-like, with a long stipe and repeated whorls of divergent phialides; primary branches of secondary conidiophores forming independent units, each terminating in adpressed phialides; several narrow conidial columns arising from one secondary conidiophore; colonies frequently with a brown stroma; conidia ovoidal..... ***C. rogersoniana*** (14)
Conidia (4.8–)5.8–6.6–7.2(–9.6) × (2.2–)3–3.2–3.8(–4.2) µm.

30 Primary conidiophores, if present, acremonium-like, with divergent phialides on short stipes, or narrowly penicillate, adpressed; secondary conidiophores absent or present, typically with somewhat divergent primary branches; colonies generally without a brown stroma; conidia of various shapes **31**

31 75 % of conidia less than 3 µm wide..... **32**

31 75 % of conidia more than 3 µm wide **34**

32 Conidia oblong ellipsoidal, hilum slightly laterally displaced; 75 % of conidia narrower than 2.5 µm; L/W of 75 % of conidia more than 2.5(–5.3); aerial mycelium abundant (OA), bearing soli-

tary, frequently densely scattered secondary conidiophores (verticillium-like primary conidiophores frequently sparse or absent in culture but frequently formed on the natural substratum, seated on perithecia or on bark close to the perithecia ..... ***B. compactiuscula*** (anamorph *C. compactiuscula*) (13)
Conidia (3.9–)5.4–6.6–7.5(–12.4) × (1.5–)1.9–2.2–2.5(–3.2) µm.

32 Conidia ellipsoidal to ovoidal, hilum median or slightly laterally displaced; 75 % of conidia wider than 2.5 µm; L/W of 75 % of conidia less than 2.5; aerial mycelium more sparsely formed **33**

33 Colonies more than 25 mm diam; primary conidiophores narrowly penicillate, adpressed; perithecia sometimes present in culture, solitary, light orange; on recently dead trees; common in tropical regions ..... ***B. grammicospora*** (anamorph *C. grammicospora*) (26)
Conidia (4–)5.4–6–6.8(–8.8) × (1.8–)2.6–2.8–3(–4) µm.

33 Colonies less than 20 mm diam; primary conidiophores rare, acremonium-like or of few divergent phialides formed on short stipes; perithecia not observed in culture; on dead branches of *Buxus* ?and *Solanum tuberosum*; temperate, Europe ..... ***B. levigata*** (anamorph *C. levigata*) (30)
Conidia (4–)5.6–6–6.4(–7.6) × (2.0–)2.4–2.6–2.6(–3) µm.

34 Colonies 5–15 mm diam; typically no growth at 27°C; conidiophores dimorphic, after subcultivations monomorphic; both types of conidiophores penicillate, adpressed; Australia and New Zealand ..... ***B. grammicosporopsis*** (anamorph *C. grammicosporopsis*) (27)
Conidia (4.8–)6.6–7.6–8.4(–11.6) × (2.2–)3–3.4–3.6(–4.6) µm.

34 Colonies 15–25 mm diam; growth at 27°C; conidiophores dimorphic; primary conidiophores verticillium-like or penicillate, adpressed **35**

35 Primary conidiophores acremonium-like or narrowly penicillate; branches of secondary conidiophores penicillate, somewhat divergent; intercalary phialides rare; conidia ellipsoidal, hilum mostly visible; temperate, Netherlands ..... ***C. intermedia*** (31)
Conidia (5.4–)6.2–8.4–9.6(–15) × (2.6–)3.2–4–4.6(–5.4) µm.

35 Primary conidiophores of slightly divergent phialides formed on short stipes; branches of secondary conidiophores divergent; intercalary phialides frequently formed below solitary terminal phialides; conidia broadly ellipsoidal, without or with a hardly visible hilum; tropical (Brazil) ..... ***C. chlorina*** (32)
Conidia (6.2–)7–7.2–7.4(–8.8) × (3.2–)3.6–4–4.2(–4.4) µm.

36(29) Primary conidiophores verticillium-like; branches and/or phialides divergent or at least divergent at acute angles; stipes long or short; long side branches sometimes arising from near the base of the main stipe **37**

36 Primary conidiophores narrowly penicillate; branches and/or phialides adpressed; stipes generally long compared to the height of the penicillus; long side branches rare or absent **44**

37 L/W of 75 % of conidia more than 2.5(–5.3); 75 % of conidia less than 2.5 µm wide; conidia almost cylindrical, straight; primary conidiophores sparsely formed or lacking in culture, frequently associated with the perithecia on the natural substratum ..... ***B. compactiuscula*** (anamorph *C. compactiuscula*) (13)
Conidia (3.9–)5.4–6.6–7.5(–12.4) × (1.5–)1.9–2.2–2.5(–3.2) µm.

37 L/W of 75 % of conidia less than 2.7 and/or 75 % of conidia wider than 2.5 µm; conidia not cylindrical; primary conidiophores abundantly formed in cultures **38**

38 Secondary conidiophores obscure or lacking; aerial mycelium generally sparsely formed ..... ***C. rosea*** f. ***rosea*** (5) or ***C. rhizophaga*** (7)
Conidia (4.8–)5.8–6.4–7(–9) × (2.4–)2.6–3–3.2(–4.2) µm.

38 Secondary conidiophores abundantly formed; aerial mycelium more abundantly formed **39**

39 Conidia hardly curved, appearing ovoidal; primary branches of secondary conidiophores somewhat divergent, forming independent units, each terminating in adpressed phialides; several narrow conidial columns arising from one secondary conidiophore; brown stroma frequently submerged to superficial, in older cultures bearing scattered secondary conidiophores ..... ***C. rogersoniana*** (14)
Conidia (4.8–)5.8–6.6–7.2(–9.6) × (2.2–)3–3.2–3.8(–4.2) µm.

39 Conidia distinctly curved, with one rounded and one flattened side; primary branches of secondary conidiophores adpressed and/or whorls of terminal phialides ± divergent, typically forming one conidial column; brown stroma absent **40**

40 75 % of conidia of the secondary conidiophores wider than 2.8–3 µm, longer than 5 µm; sporodochia or sporodochial pustules generally formed in culture; New Zealand, Japan **41**

40 75 % of conidia of the secondary conidiophores less than 2.8–3 µm wide, shorter than 6 µm; sporodochia or sporodochial pustules present or absent in culture; holomorphs mainly tropical, anamorph also temperate..... **43**

41 Phialides of secondary conidiophores and sporodochial conidiophores mostly adpressed; intercalary phialides frequent below the terminal phialides; only known from ascospore isolations; teleomorph on *Rhopalostylis sapida*; New Zealand..... ***B. verrucispora*** (anamorph *Clonostachys verrucispora*) (12)
Conidia (5.6–)7.4–8.4–9.2(–15.6) × (2.2–)3–3.2–3.6(–4.4) µm.

41 Branches and phialides of secondary conidiophores and at least of young sporodochia ± divergent; intercalary phialides rare or absent **42**

42 Temp. maximum for growth 30°C; stipes of primary conidiophores frequently shorter than the branched part; only known from ascospore isolations; teleomorph on recently dead trees; New Zealand ..... ***B. zelandiaenovae*** (anamorph *C. zelandiaenovae*) (11)
Conidia (4–)5.2–6–6.4(–13.2) × (2.4–)2.8–3–3.2(–4.2) µm.

42 Temp. maximum for growth 33°C; stipes of primary conidiophores generally longer than the height of the branched part; Japan ..... ***B. capitata*** (anamorph *C. capitata*) (8)
Conidia (4.6–)6–6.8–7.2(–12.4) × (2.2–)2.8–3.2–3.4(–4.2) µm.

43 Primary conidiophores variably branched, frequently with long side branches arising from near the base; phialides generally divergent in narrow angles; secondary conidiophores variable: stipes distinct or short and merging gradually into strands of aerial mycelium; sporodochia frequently formed; conidial columns of secondary conidiophores and on sporodochia early collapsing to slimy, flat dome-shaped masses; intercalary phialides rare or absent; common in tropical, rare in temperate regions; perithecia not observed in culture .... ***B. byssicola*** (anamorph *C. byssicola*) (6)
Conidia (3.2–)4.4–5.2–5.8(–10.8) × (1.8–)2.4–2.6–2.8(–4) µm.

43 Primary conidiophores constantly verticillium-like, side branches rarely arising from near the base; stipes generally longer than the height of the branched part; phialides clearly divergent (if adpressed and formed on divergent metulae, go to 44a); secondary conidiophores with distinct stipes, generally solitary to aggregated; sporodochial clusters rare or absent; imbricate conidial chains generally slender and long, typically not collapsing on adjacent conidiophores; intercalary phialides absent or rarely formed below whorls of terminal phialides; perithecia frequently observed in colonies isolated from ascospores, not observed in those isolated from conidia; from temperate regions ..... ***B. ochroleuca*** (anamorph *C. rosea*) (5)
Conidia (4.2–)4.8–5.2–5.6(–6.6) × (2–)2.4–2.8–3(–3.4) µm (those from primary conidiophores to 15.4 µm long).

43 Stipes of both kinds of conidiophores mostly shorter than the branched part; branches of secondary conidiophores ± divergent; intercalary phialides below terminal phialides rarely present; sporodochia absent; India..... ***C. agrawalii*** (9)
Conidia (3.8–)4.2–4.6–4.8(–5.8) × (2.2–)2.4–2.6–2.9(–3) µm.

44(36) Phialides of primary conidiophores adpressed; metulae and branches adpressed or divergent at acute angles; branches of secondary conidiophores adpressed; conidiophores solitary; sporodochia absent; pantropical and Australia..... ***B. pseudochroleuca*** (anamorph *C. pseudochroleuca*) (17)
Conidia (3.2–)4–4.4–4.6(–6.4) × (1.2–)2.2–2.2–2.4(–3) µm.

44 Branches and phialides of primary conidiophores entirely adpressed; secondary conidiophores, if present, with ± divergent branches, solitary, densely aggregated, confluent and forming sporodochial aggregates **45**

45 Colonies mostly slow-growing, less than 10 mm diam in 7 d; secondary conidiophores rare, difficult to see among the primary conidiophores, in fresh isolates, forming sporodochial aggregates; only known from ascospore isolations; New Zealand and Australia ..... ***B. aureofulvella*** (anamorph *C. aureofulvella*) (16)
Conidia (3.6–)4.8–5.8–7(–9) × (1.8–)2.4–2.8–3.2(–3.8) µm.

45 Colonies growing faster, 20–30 mm diam in 7 d; secondary conidiophores abundant, solitary or aggregated; sporodochial aggregates commonly formed from strands of aerial mycelium..... **46**

46 Conidial masses whitish to pale orange to orange-brown; holomorph common in tropical, rare in temperate regions; anamorph common in temperate regions ..... ***B. solani*** (anamorph *C. solani*) (15)
Conidia (3.8–)4.4–4.8–5(–6.8) × (2–)2.4–2.6–2.8(–3.8) µm (those from primary conidiophores to 10 µm long).

46 Conidial masses pale orange to brown; only known from ascospore isolations; Asia (Indonesia, Japan)..... ***B. pseudostriata*** (anamorph *C. pseudostriata*) (18)
Conidia (3.6–)5–5.6–6.2(–8) × (2–)2.6–3–3.2(–3.8) µm.

5. Key to species of the *Bionectriaceae* with greenish conidial masses based, mainly on characters of the ascomata

1 Sterile, branched, filamentous elements visible among mature asci; ascospores striate or smooth, one- to pluriseptate **2**

1 Sterile elements among the asci absent; ascospores smooth, rough, or warted, 1-septate **5**

2 Ascospores pluriseptate, striate..... ***Peethambara spirostriata*** (*Bionectriaceae*) (anamorph *Didymostilbe echinofibrosa* (E.F. Morris) Rossman) (Rossman, 1983; Rossman *et al*., 1999)

2 Ascospores 1-septate, smooth, rough, or striate **3**

3 Ascospores smooth, reniform, 31–42 ×14.5–21 µm..... ***Peethambara sundara*** (*Bionectriaceae*) (anamorph *Didymostilbe sundara* (Subram. & D.J. Bhat) Seifert) (Subramanian & Bhat, 1978; Seifert, 1985)

3 Ascospores striate, less than 20 µm long **4**

4 Ascospores mostly wider than 4 µm; conidia 0-septate..... **'*Nectria*'** (?*Peethambara*) ***chlorogloea*** .....(?*Bionectriaceae*; anamorph myrothecium-like) (Samuels, 1988b)
Ascospores (12–)14–15.8–17(–19.8) × (3.6–)4–4.6–5(–5.6) µm.

4 Ascospores mostly narrower than 4 µm; conidia 1-septate ..... **'*Nectria*' *septomyrothecii*** Samuels (?*Bionectriaceae*) (anamorph *Septomyrothecium* Matsush.) (Samuels, 1988b)
Ascospores (12.6–)14–15.4–16(–18.2) × (2.8–)3.2–3.4–3.4(–3.8) µm.

5 Ascospores warted, slightly unevenly 2-celled, with one end slightly tapering, the other slightly more rounded, shorter than 16 µm; perithecia less than 200 µm diam..... ***Bionectria*** **subgenus** ***Astromata*** (22–24)

5 Ascospores smooth or rough, not conspicuously warted, uniformly 2-celled, straight or bean-shaped; 75 % of ascospores longer than 16 µm; perithecia more than 300 µm diam **6**

6 Ascospores ± straight, both ends slightly tapering, at least not broadly rounded; 75 % of ascospores shorter than 20 µm; conidia wider than 4 µm; at least 75 % of conidia longer than 10 µm; conidial wall deeply pigmented ..... ***Bionectria ralfsii*** (21)

6 Ascospores bean-shaped, both ends broadly rounded; 75 % of ascospores longer than 20 µm; conidia less than 4 µm wide, shorter than 9 µm; conidial wall greenish hyaline, not deeply pigmented ..... ***Bionectria pityrodes*** (25)

6. Key to anamorphs with greenish pigmented conidial masses

1 Conidiomata with free-ending, sterile hyphal elements or setae **2**
1 Conidiomata without differentiated, free-ending, sterile hyphal elements **6**

2 Conidiomata sporodochial **3**
2 Conidiomata synnematous **5**

3 Sterile elements of curled, branched and frequently verrucose, marginal hyphae and/or relatively thick-walled and wide setae ..... ***Myrothecium*** *sensu* Tulloch (1972)
3 Sterile elements not differentiated, of similar dimension to the cells of the conidiophores **4**

4 Conidiomata with a differentiated margin because of a palisade of hyphae or conidiophores extending beyond the hymenium, thus cupulate; conidia 1-celled, ellipsoidal to ovoidal, symmetrical; hilum hardly visible ..... ***Bionectria pityrodes*** (25)
4 Conidiomata not cupulate; sterile hyphae solitary, extending markedly beyond the hymenium; conidia 1-septate, cylindrical, slightly curved ..... **'*Nectria*'** (?*Peethambara*) ***septomyrothecii*** (Samuels, 1988b)

5 Sterile elements short, formed at the margin of the synnema stipe, not protruding beyond the hymenium, with frequently swollen, verrucose end-cells, rarely absent; hyphae of stipe densely aggregated, frequently and particularly in the lower part darkly pigmented; conidia 1- or 2-celled; conidial wall frequently pigmented, smooth or somewhat striate; teleomorph in *Peethambara* or unknown; on leaves or bark of plants ..... ***Didymostilbe*** (Seifert, 1985)
On grasses ..... ***Myrothecium masonii*** (Tulloch, 1972)
5 Sterile elements simple, not swollen, hypha-like, protruding beyond the hymenium; hyphae of synnema stipe smooth, loosely aggregated, not pigmented; conidia 1-celled, smooth, with hyaline, not deeply pigmented walls; on bark ... **'*Nectria*'** (?*Peethambara*) ***chlorogloea*** (Samuels, 1988b)

6(1) Conidiomata sporodochial to robust synnematous, sometimes widening in the upper part, funnel-shaped; wall of conidia deeply pigmented; conidia lemon-shaped, the distal end somewhat apiculate ..... ***Bionectria ralfsii*** (21)
6 Conidiomata flat, sporodochial, not synnematous; conidia greenish hyaline, of various shapes **7**

7 Conidia straight (oval to ellipsoidal), almost homopolar, hilum median or invisible; phialides cylindrical or very slightly widening towards the tip, narrowing just below the apex, therefore the tip appearing somewhat rounded ..... ***Bionectria pityrodes*** (25)
7 Conidia slightly curved, at least near the base, hilum more or less laterally displaced or slightly extruding (ellipsoidal to clavate); phialides oblong flask-shaped to cylindrical, slightly narrowing towards the apex, apical part straight, not sharply tapering below the apex **8**

8 Conidiophores of conidiomata penicillate, adpressed, or of phialides seated on aggregates of angular cells, or of phialides seated on short supporting cells that are scattered laterally on hyphae; branches and phialides frequently paired on their supporting cell; conidia ellipsoidal to clavate, with a slightly laterally extruding base ..... ***Bionectria*** subgenus ***Astromata*** (22–24)
8 Branches of conidiophores strongly divergent, almost rectangular; conidia slightly curved, hilum laterally displaced, not extruding ..... ***Clonostachys divergens*** (20)

DESCRIPTION OF THE TAXA

BIONECTRIA Speg., *Bol. Acad. Ci.* (*Córdoba*) 23: 563. 1919.

Anamorphs: ***Clonostachys*** Corda, Prachtflora europäischer Schimmelbildungen, p. 31, pl. 15, Figs 1–4. 1839.

= *Spicaria* Harting, Nieuwe Verh. Kon. Inst. Wet. Amsterdam 12: 226. 1846.
= *Dendrodochium* Bonorden, Handb. allg. Mykol.: 135. 1851; Pl. 228, a, b *in* Abhandlungen aus dem Gebiete der Mykologie. Zweiter Theil. 1870.
= *Clonostachyopsis* Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1, 116: 148 (Fragm. Mykol. 3: No. 147: 66) 1907.
= *Gliocladochium* Höhn., Mitt. Bot. Inst. Techn. Hochsch. Wien. 3: 4. 1926.
= *Verticilliodochium* Bubák, Ann. Mycol. 12: 220, pl. 8: 1–6. 1914.
= *Sesquicillium* W. Gams, Acta Bot. Neerl. 17: 455. 1968.
Additional anamorphs: Gliocladium- or myrothecium-like.

Stroma well-developed, erumpent through bark, pseudoparenchymatous or prosenchymatous (subgenera *Bionectria*, *Zebrinella*, *Myronectria*) or superficial, prosenchymatous to hyphal, forming a perithecial base (subgenera *Epiphloea, Uniparietina*) or absent (subgenus *Astromata*). **Perithecia** superficially free, not immersed; solitary to densely crowded in numbers of up to 100 on erumpent stroma forming clusters of 3 mm diam or solitary on a superficial stroma; globose to subglobose, frequently somewhat higher than wide, 200–500 µm diam or 150–250 µm in subgenera *Uniparietina* and *Astromata*; not or minutely papillate, mostly laterally pinched or not pinched when dry, rarely apically pinched; pale yellowish, pale orange, orange or brownish orange, rarely brown, KOH-negative, frequently with a more intensely pigmented, slightly darker ostiolar region when dry; smooth or warted. **Perithecial warts**, if present, covering the subapical and lateral parts of the perithecial wall, sometimes radiating from the apex, usually best developed around the ostiole, generally less pigmented than the perithecial wall, off-white to tan, rarely pale yellowish; cells of warts angular to subglobose (subgenus *Bionectria*) or globose to subglobose (subgenus *Zebrinella*), hardly distinct from the cells of the outer perithecial wall region, generally without vacuoles, with either uniformly thin (subgenus *Zebrinella*) or unevenly thickened (subgenus *Bionectria*) walls; thickened walls facing outwards. **Setae** arising from the perithecia generally absent or (in subgenus *Uniparietina*) short, somewhat undulate, not conspicuously thick-walled, hyphal. **Perithecial wall** of one (subgenus *Uniparietina*), two (subgenera *Zebrinella*, *Epiphloea, Uniparietina*), or three (subgenera *Bionectria*, *Myronectria*) regions. **Inner region** always present, lining the inner surface of the perithecium and the ostiole, bearing inside subapically brick-like cells from which the periphyses arise; cells flat in sections, lobed to rarely subglobose in subsurface view, with unevenly thickened walls that are very thin at several spots of the cell, resulting in 'pseudopores' between adjacent cells. **Middle region** present in most species of subgenera *Bionectria* and *Myronectria*, consisting of one or few layers of intertwined hyphae, inconspicuous in sections, forming a *textura intricata* in subsurface view, observable mainly in the lateral and subapical parts of the perithecium. **Outer region** only absent in subgenus *Uniparietina*, consisting of angular or subglobose to globose cells, frequently containing light-coloured drops, 2–5(–7) cells thick, forming a *textura angularis* or *globulosa* in section and (sub)surface view, surrounding all of the perithecium, except the ostiole; cells in subgenus *Bionectria* intergrading with those of the warts and the erumpent stroma, in subgenera *Zebrinella* and *Epiphloea* only with those of the warts; outermost cell layer differentiated only in subgenera *Epiphloea* and *Uniparietina*, epidermoidal to somewhat hyphal. **Asci** narrowly clavate to clavate, mostly 8-spored, rarely less than 8-spored when spores are long; apex narrowly to broadly rounded or truncate, sometimes with prominent edges, typically with an apical, horizontal ring, or simple, lacking a visible ring if ascospores are large. **Ascospores** 2-celled (1-celled in *B. coronata*), ellipsoidal, generally with slightly tapering ends, rarely with broadly rounded ends; spinulose to warted, or striate, rarely smooth, not constricted or slightly constricted at the septum with age, colourless, uniseriate below, biseriate above, filling the ascus almost completely.

Mononematous conidiophores dimorphic (referred to as primary or secondary conidiophores) or monomorphic, mononematous or sporodochial, smooth, hyaline. **Primary conidiophores** verticillium-like or narrowly penicillate (**gliocladium-like**), or acremonium-like, solitary, producing round, watery, more or less colourless conidial heads. **Secondary conidiophores** adpressed penicillate or loosely, ± divergently branched, mononematous, densely aggregated, and/or distinctly sporodochial forming chains or columns of imbricate conidia that may collapse to slimy masses. **Sporodochia** robust, rarely somewhat synnematous, only cupulate in *B. pityrodes* because of a palisade of sterile or conidiogenous cells that extend slightly beyond the hymenium; sporodochial subhymenium forming a *textura porrecta*, or sometimes, particularly in culture, a *textura intricata*; sporodochia in species of subgenus *Astromata* can consist of phialides aggregated on angular to globose cells or on short supporting cells that are scattered laterally on swollen hyphae (referred to as **small-sporodochial**); sporodochia with white to brownish conidial masses

are referred to as **dendrodochium-like**, those with green-coloured masses as **myrothecium-like**. **Conidiogenous cells** always phialidic, cylindrical to flask-shaped, straight or slightly curved; apical part ± straight, tip with periclinal thickening, truncate, rarely narrowing just below the apex; intercalary phialides absent, rarely formed below whorls of terminal phialides, formed below solitary, terminal phialides (**sesquicillium-like**). Conidial masses uncoloured (white), pale yellow, pale to light orange, brownish orange, rarely brown or pale to dark green. **Conidia** 1-celled (partly 1-septate in one species, *C. setosa*), smooth, elongate, slightly curved because of one somewhat flattened side, with a laterally displaced hilum, or almost straight, ovoidal to ellipsoidal, with an almost median or invisible hilum, hyaline or greenish hyaline, only in *B. ralfsii* with more deeply pigmented, dark green walls.

Vegetative mycelium on the natural substratum sparsely developed, absent, or visible as a thin superficial mat when perithecia are formed superficially (subgenus *Epiphloea*), or subcortical, running parallel to the surface of the bark when perithecia and/or sporodochia are formed on an erumpent stroma. **Perithecia** mostly not produced in culture; in some species solitary, in clusters on a stroma, from aerial mycelia, or on the agar surface, homothallic.

Habitat: Ascocarps on bark of recently dead trees, decaying leaves, rarely lichens, frequently close to or on fungal hosts, particularly ascomycetes, or with stroma incorporating a host; anamorphs associated with teleomorphs on various decaying plant materials or obtained separately when soil-borne. Some species known as destructive mycoparasites, growing on or in the host mycelium, sometimes on animal substrata.

Type species: *Bionectria tonduzii* Speg.

Published descriptions: Rossman *et al*. (1999), Samuels (1976a, *Nectria ochroleuca*-group, here subgenus *Bionectria*), Samuels (1988b, *N. grammicospora* and allies, here subgenus *Zebrinella*), Samuels (1989, *N. sesquicillii* and allies, here subgenus *Epiphloea*), Schroers & Samuels (1997), Schroers *et al*. (1999b).

Notes: *Bionectria* is characterized by ± light orange, KOH-negative perithecia formed on lignicolous or herbaceous substrata, frequently on or associated with other ascomycetes, indicating a mycoparasitic or mycosaprobic life-style. The teleomorphs are variable in perithecial wall anatomy, stroma morphology, and ascospore ornamentation. To account for the different character patterns of the teleomorphs, several subgenera are proposed. Typical characters of *Bionectria* include superficially free perithecia [not immersed in the substratum or in pseudoparenchymatous or hyphal cells as occur in several other genera of the *Bionectriaceae* (*Clibanites* P. Karst., *Mycocitrus* A. Möller, *Nectriopsis* Maire, *Protocreopsis* Doi, *Selinia* P. Karst., *Stilbocrea* Pat., or *Valsonectria* Speg.)]; only in *Bionectria* subgenus *Uniparietina* do seta-like hyphae arise from the outer perithecial wall (as for example in *Dimerosporiella* Speg., *Hydropisphaera* Dumort., *Ijuhya* Starbäck, *Nectriopsis*, and *Trichonectria* Kirschst.). Perithecia in *Bionectria* generally pinch laterally when dry (not apically as for example in *Hydropisphaera*) and no intercellular drops are found (as in *Ochronectria* Rossman & Samuels). Other characters such as the occurrence of well-developed erumpent stromata, relatively fleshy perithecial walls, warted perithecia, and the occurrence of cells with unevenly thickened walls, are rare in other taxa of the *Bionectriaceae*, although they do not occur in all species or species groups of *Bionectria*. Taxa that are similar in certain features, such as perithecial habit and warts, are found for example in the *Nectriaceae*, like *Nectria* and *Albonectria*. More unique characters of *Bionectria* are found in the anamorphs that all share the basic construction of a penicillate conidiophore (whether or not accompanied by synanamorphs), arranged in sporodochia or forming intercalary phialides, and the imbricate arrangement of conidia. These characters unite all anamorphs to the broadly delimited genus *Clonostachys* but terms like gliocladium-, sesquicillium-, dendrodochium-, myrothecium-, or small-sporodochial are used to emphasize morphological variations. Other genera in the *Bionectriaceae* contrast by mainly acremonium-like or synnematous anamorphs that form conidia in slimy masses or round heads (Rossman, 2000). For the distinction of *Bionectria* from gliocladium-like anamorphs found in other genera such as *Roumegueriella*, *Rhopalocladium* Schroers, Samuels, & W. Gams (anamorph of *Nectriopsis sporangiicola*) (both *Bionectriaceae*) and *Gliocladium sensu stricto* (anamorph of *Sphaerostilbella* and related taxa) (*Hypocreaceae*), other characters such as conidial size, morphology of the cells in the penicilli, ornamentation of the conidiophore stipe, life-style, colony characters and associated teleomorphs need to be considered (Schroers *et al*., 1999b). The pigmentation of conidial masses, particularly the distinction between green and white to orange colours, is of minor significance for the generic delimitation of *Bionectria*.

To account for differences in teleomorphs of species accepted for *Bionectria*, six subgenera are proposed:

(i) *Bionectria* subgenus *Bionectria* (anamorphs *Clonostachys s.s*, dendrodochium-like, myrothecium-like, rarely sesquicillium-like).

(ii) *Bionectria* subgenus *Zebrinella* (anamorphs *Clonostachys s.s*., sesquicillium-like, gliocladium-like).

(iii) *Bionectria* subgenus *Astromata* (anamorphs myrothecium-like or small-sporodochial).

(iv) *Bionectria* subgenus *Myronectria* (anamorph myrothecium-like).

(v) *Bionectria* subgenus *Epiphloea* (anamorphs sesquicillium-like).

(vi) *Bionectria* subgenus *Uniparietina* (anamorphs sesquicillium-like).

BIONECTRIA SUBGEN. BIONECTRIA — Species 1–21.

Anamorphs: ***Clonostachys***, conidiophores typically dimorphic, secondary conidiophores rarely with intercalary phialides (sesquicillium-like), conidiomata sporodochial (dendrodochium- or myrothecium-like).

Stroma well-developed, erumpent through bark, rarely through or on the outer cortex of herbaceous plants; cells pseudoparenchymatous. **Perithecia** crowded in groups of 3–50(–100), rarely solitary, smooth or warted; cells of warts frequently with unevenly thickened walls. **Perithecial wall** 45–90 µm thick, consisting of three, rarely two regions. Outer region formed by angular to subglobose, pseudoparenchymatous cells; cells of the outer region, stroma, and perithecial warts similar in shape, frequently containing orange droplets. Middle region hyphal, lacking in some species. **Ascospores** coarsely or finely warted, rarely smooth, hyaline, 1-septate, rarely 2-septate at maturity. **Conidiophores** mostly dimorphic, rarely monomorphic, mononematous, or aggregated in pustules. Primary conidiophores verticillium-like or adpressed penicillate, bearing watery, unpigmented or greenish heads of conidia. Secondary conidiophores penicillate, adpressed or with more or less divergent branches, solitary, aggregated or sporodochial, sometimes with intercalary phialides formed below whorls or solitary phialides, bearing ± imbricate chains or columns of conidia. Conidial masses of the secondary conidiophore white, pale yellowish, pale orange, to greenish. **Conidia** slightly curved, with a laterally displaced hilum, frequently 5–6 × 2.5–3 µm, in few species longer and to 15 × 7 µm. **Sporodochia** particularly occurring on the natural substratum on an erumpent stroma that bears a well-developed subhymenium of hyphae arranged in a *textura porrecta*; in cultures present or absent, cushion-shaped, generally without a stroma, and with a subhymenium of hyphae arranged in a *textura intricata*; conidia on sporodochia initially in chains or columns, generally collapsing to slimy masses.

Known distribution: Teleomorphs tropical to subtropical, rarely temperate. Some anamorphs cosmopolitan, many known only from ascospore isolates.

Habitat: Teleomorphs on bark of recently dead trees, rarely on decaying leaves, frequently close to or on fungal substrata, particularly ascomycetes, or with stroma incorporating a host. Conidiophores scattered solitarily on bark or perithecial stroma; sporodochia, if present, frequently formed independently but close to the perithecial stroma. Anamorphs frequently isolated from decaying plant materials or soil-borne; some species known as destructive mycoparasites, growing on, coiling around, penetrating into, and growing inside of the host mycelium; a few isolates obtained as parasites on ticks, slugs, or growing on dead insects or keratinoid substrata.

Published descriptions: Rossman *et al*. (1999), Samuels (1976a), Schroers & Samuels (1997), Schroers *et al*. (1999b).

Notes: Dingley (1957) firstly assumed a close relationship of some of the species that are here classified in *Bionectria* subgenus *Bionectria*. Booth (1959) established the *Nectria ochroleuca*-group for three British species similar to those discussed by Dingley (1957), characterized by a well-developed stroma bearing superficially crowded perithecia. He attributed the anamorphs to *Gliocladium* and described dimorphic conidiophores (1959: p. 40, Fig. 12) for one species, *N. solani*, with reference to Petch (1944). Samuels (1976a) and Samuels *et al*. (1990) revised the *N. ochroleuca*-group and included several tropical species. Samuels (1988a) was the first to emphasize morphological similarities of species of the *N. ochroleuca*-group to *B. tonduzii*. Since 1990, the *N. ochroleuca*-group comprised 11 species, most of which are here accepted in subgenus *Bionectria* or transferred to other subgenera of *Bionectria*. Samuels assigned the mostly unnamed anamorphs to *Gliocladium*, *Dendrodochium*, *Myrothecium*, or *Clonostachys*.

Species of subgenus *Bionectria* are similar in habit and anatomy of the ascocarps, ascospore ornamentation, morphology of the anamorph such as shape of conidia, and conidiophore morphology. Four species groups, however, can be distinguished within the subgenus *Bionectria* characterized by

(1) relatively long ascospores (mostly longer than 16.5 µm) and conidia (mostly longer than 7.5 µm), and an inconspicuous conidiophore dimorphism (species allied with *B. tonduzii*, species 1–4),

(2) relatively short ascospores (mostly shorter than 17 µm) and conidia (mostly shorter than 7.5 µm), a distinct conidiophore dimorphism, and primary conidiophores with divergent phialides (species allied with *B. ochroleuca*, species 5–14),

(3) as in group 2 but with narrowly adpressed, and penicillate primary conidiophores (species allied with *B. solani*, species 15–18), and

(4) entirely sporodochial anamorphs (species 19–21).

Apart from *B. compactiuscula* and *C. rogersoniana*, all species of the groups 1–3 form a monophyletic group (Figs 2–4: A). The groups 1–3 are paraphyletic or polyphyletic within this clade (Fig. 4 b).

The three species of group 4 are morphologically heterogeneous. Two of them, *B. samuelsii* and *C. divergens*, appear closely related to *C. rogersoniana*, which morphologically belongs to group 2 (Fig. 4 b).

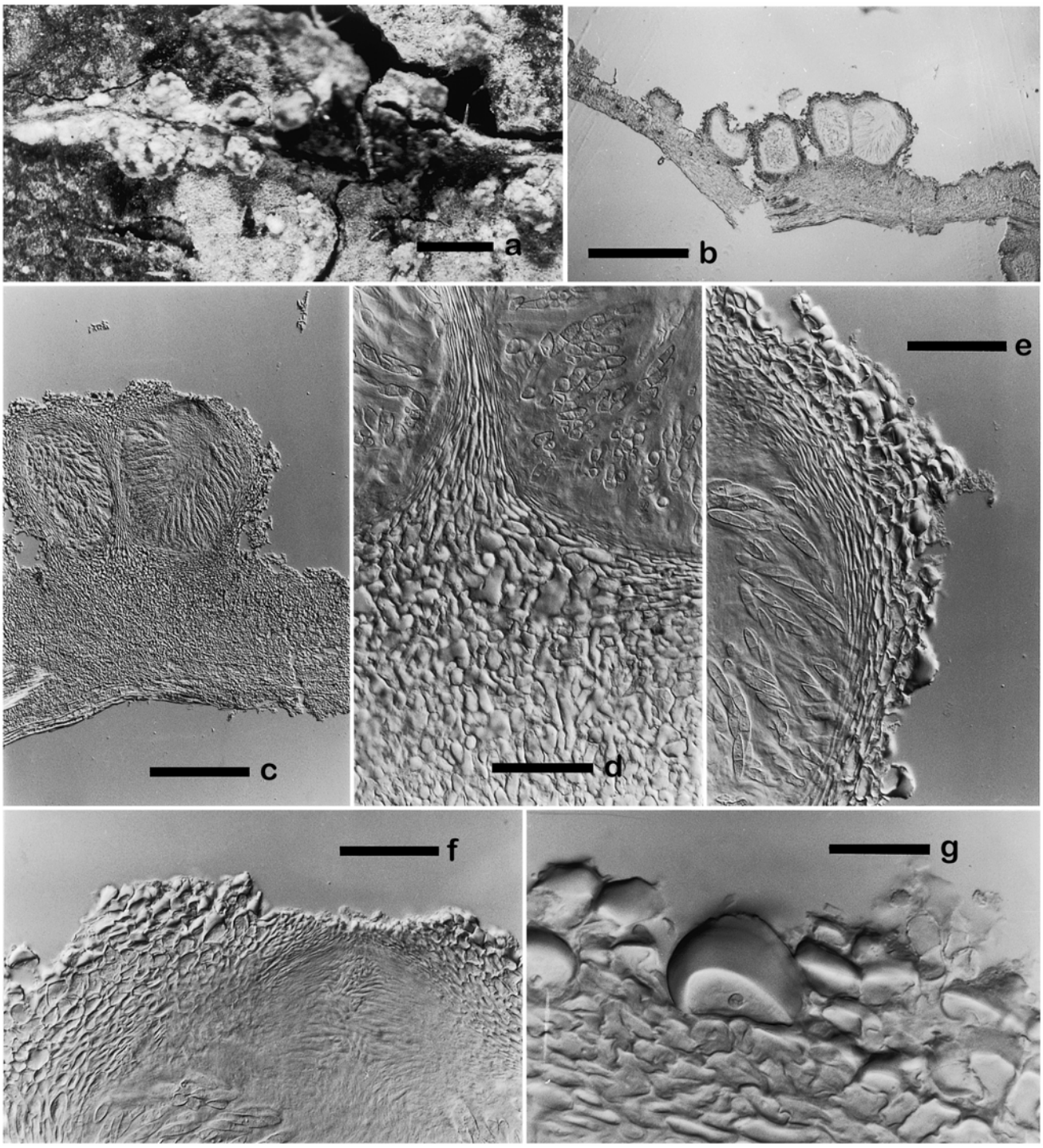


Fig. 6. ***Bionectria tonduzii*****. a.** Habit of crowded perithecia seated on a stroma along leaf vein. **b–f.** Sections through perithecia and stroma. **d.** Stroma below perithecia. **e.** Lateral perithecial wall showing two regions. **f.** Perithecial apex with small warts. **g.** Cells from perithecial surface with unevenly thickened wall. – All from Tonduz No. 1644, natural substratum. a: LM; b: DM; c–g: DIC. Scale bars: a, b = 500 µm, c = 200 µm, d–f = 50 µm, g = 20 µm.

The subgenus *Bionectria* contains 5 species that form green-coloured conidial masses. These are: (i) *C. rosea* f. *catenulata*, *C. solani* f. *nigrovirens*, and *C. rhizophaga* (green pigmentation confirmed for one strain), all three forming dimorphic conidiophores, and (ii) *B. ralfsii* and *C. divergens*, both forming sporodochia.

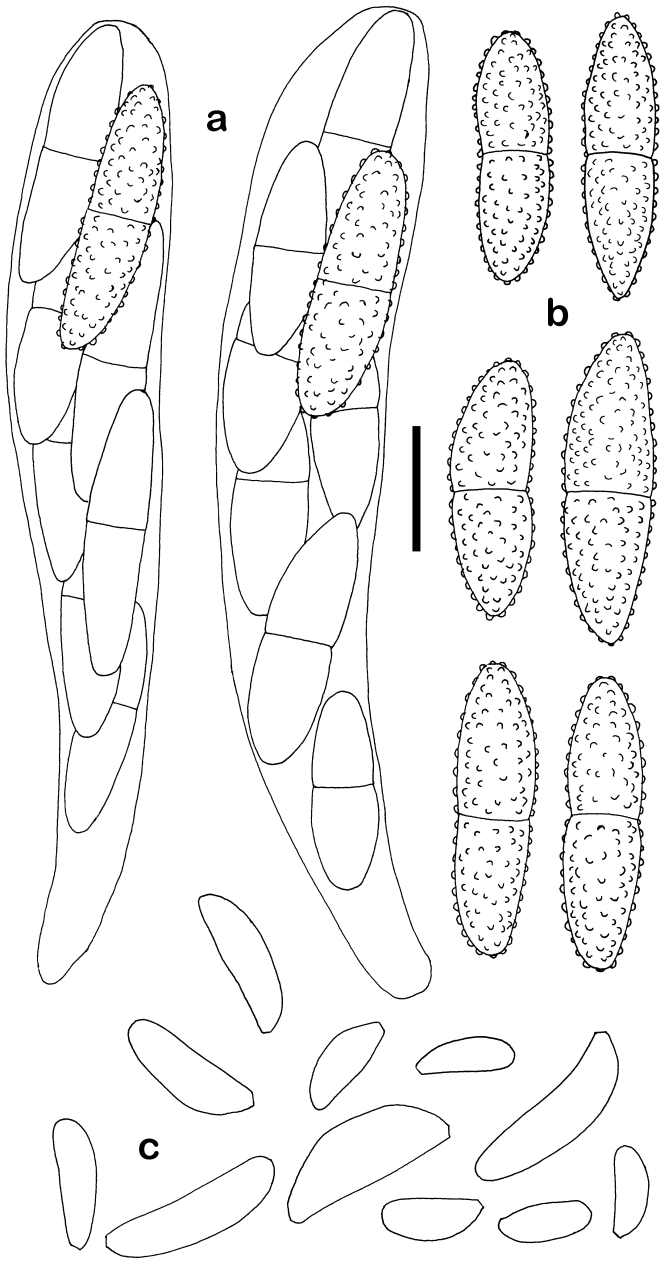


Fig. 7. ***Bionectria tonduzii***, ***Clonostachys*** ?***macrospora*****.** **a.** Almost mature asci. **b.** Discharged ascospores. **c.** Conidia associated with perithecia (anamorph–teleomorph connection not proven). – All from Tonduz No. 1644, natural substratum. Scale bar (applying to all structures) = 10 µm.

1. Bionectria tonduzii Speg., Bol. Acad. Ci. (Córdoba) 23: 563. 1919 (as '*tonduzi*'). — Figs 6 a–g, 7 a–c.

≡ *Nectria tonduzii* (Speg.) Samuels, Mem. New York Bot. Gard. 48: 22. 1988.

Anamorph: ***Clonostachys*** ?***macrospora*** (Sacc. & Ellis) Schroers & W. Gams. — Fig. 7 c (connection not conclusively proven, based on a few conidia found on the original specimen).

Description from natural substratum: Stroma erumpent between cells of the leaf epidermis, or superficial, 30–100 µm high, rather flat, with cells of 6–15 × 5–10 µm, close to or on black fungal stroma. **Perithecia** solitary to aggregated in groups of up to 15, 270–340 µm diam, oval to globose, slightly laterally pinched when dry, brownish orange, not papillate, with warted surface. **Perithecial warts** best developed in the upper part, near the ostiole, brownish grey to tan; cells 12–29 × 10–22 µm, with unevenly thickened walls up to 12 µm thick. **Perithecial wall** 30–45 µm thick, composed of two regions. Middle region of intertwined hyphae not observed. Outer region 15–25 µm or 2–3 cells thick; cells angular to subglobose, 9–18 × 5–13 µm, with uniformly thickened walls up to 1 µm thick. Inner region 15–20 µm thick. **Asci** clavate, (68–)75–82–89(–100) × (12–)13(–15) µm (n = 12), 8-spored; apex narrowly or broadly rounded, simple, without visible ring. **Ascospores** ellipsoidal to oblong-ellipsoidal, warted, (19.6–)21.2–22.6–23.4(–26) × (5.4–)5.8(–7) µm (n = 28). **Sterile mycelium** whitish to brownish grey, spreading on the leaf surface, surrounding the perithecial base. **Associated conidia** ellipsoidal, slightly curved, distally broadly rounded, with a laterally displaced hilum, (6.8–)8–9.8–11.6 (–15.4) × (2.6–)3.2–3.4–3.8(–5.8) µm (n = 27).

Type: COSTA RICA. San José; on *Buettneria carthagensis*; Oct 1894; A. Tonduz (LPS, No. 1644).

Known distribution: Costa Rica, known only from the type collection.

Habitat: On leaves of *Buettneria carthagensis* Jacq., possibly practising perithecia of *Puiggarina costaricensis* Sydow (Samuels, 1988a).

Published descriptions and illustrations: Samuels (1988a), Schroers & Samuels (1997).

Notes: The relationship of *Bionectria tonduzii* to *B. ochroleuca* and allied taxa was first suggested by Samuels (1988a). *Bionectria tonduzii* has warted perithecia (Fig. 6 a) and warted ascospores (Fig. 7 b). Relatively large ascospores, large cells with unevenly thickened walls (Fig. 6 g) covering the perithecial warts, and its occurrence on leaves of a still living plant distinguish this species. The genus *Bionectria* was originally proposed based on its purported lifestyle as a plant-parasite (Spegazzini, 1919). The perithecia, however, are seated on the stroma of another ascomycete (Samuels, 1988a), which possibly is the primary substratum of *B. tonduzii*. No anamorph can be linked unambiguously to *B. tonduzii*. However, some conidia found on the natural substratum indicate a relationship to other species of the genus because they are slightly curved and show a laterally displaced hilum (Fig. 7 c). The ascospores are 1-septate; a few of the discharged ascospores, however, have additional septa. This phenomenon is considered not significant and pluriseptate ascospores are not considered typical

of the genus *Bionectria*. *Bionectria tonduzii* is most similar to *B. apocyni* in habit of the perithecia, ascospore size, perithecial wall anatomy and conidial size range. It is likely that *B. tonduzii* is a synonym of *B. apocyni*.

2. **Bionectria apocyni** (Peck) Schroers & Samuels, Z. Mykol. 63: 153. 1997. — Figs 8 a–i, 9 a, 10 a, b.

≡ *Nectria apocyni* Peck, Bull. Buffalo Soc. Nat. Sci. 1: 71. 1873.
≡ *Cucurbitaria apocyni* (Peck) O. Kuntze, Rev. Gen. Plant. 3: 460. 1898.
= *Nectria rugispora* Pat., Bull. Trimestriel Soc. Mycol. France 8: 133. 1892.
= *Nectria carneoflavida* Penz. & Sacc., Malpighia 11: 511. 1897.
?= *Nectria ambigua* Penz. & Sacc., Malpighia 11: 511. 1897.

Anamorph: ***Clonostachys macrospora*** (Sacc. & Ellis) Schroers & W. Gams, *comb. nov.* — Figs 9 b–d, 10 c–e.

≡ *Dendrodochium macrosporum* Sacc. & Ellis, Michelia 2: 580. 1882.
= *Dendrodochium roseomucosum* Matsush., Matsush. Mycol. Mem. 8: 17. 1995.

Description from natural substratum: Stroma subcortical, erumpent through the bark of woody plants or the exoderm of herbaceous plants, or superficial, rather flat, bearing small sporodochia or perithecia; cells angular to somewhat prosenchymatous. **Perithecia** loosely to densely crowded in groups of 3–20 (rarely more), globose to subglobose, to 500 µm diam, not or minutely apically pinched when dry, golden-orange to brownish orange, not or minutely papillate, scaly to warted, particularly in the upper part and around the ostiole. **Perithecial warts** *ca* 30 µm high and *ca* 60 µm diam, whitish to tan; cells intergrading with those of the perithecial wall; outermost cells (5–)10–11–13 (–17) × (4–)7–8–9(–14) µm with unevenly thickened walls up to 8 µm thick. **Perithecial wall** 35–80 µm thick, composed of two or three regions. Outer region 25–53 µm or to 5 cells thick; cells angular to subglobose, 8–23 × 5–18 µm, frequently containing vacuoles, with uniformly thickened walls around 1.5 µm thick. Middle region obscure, not seen in all specimens, probably consisting of only 1 layer of intertwined hyphae. Inner region 11–25 µm thick. **Asci** narrowly clavate, slightly tapering towards the apex, (55–)80–85–100(–120) × (8.5–) 12.0–13.5–15.0(–19.5) µm (n = 158); apex rounded or flat, edges frequently protruding, ring visible or not visible, commonly seen in young asci but inconspicuous in mature asci; some specimens containing asci with reduced numbers of ascospores. **Ascospores** ellipsoidal to oblong-ellipsoidal, typically tapering towards the ends, equally 1-septate, conspicuously warted, frequently with a larger wart at the tip, (16–)20.6–22.6–24.6(–32) × (4.6–)6–6.8–7.6(–9.4) µm (n = 433). **Sterile mycelium** invisible. **Sporodochia** frequently associated with perithecial clusters, mostly higher than broad and somewhat widening upwards; hyphae of subhymenium forming a *textura porrecta*; base pseudoparenchymatous. Most temperate specimens only contain sporodochia and no perithecia.

Description from culture: Colonies reaching 30–35 mm diam in 7 d at 24ºC on all media; optimum for growth 24–27°C (35–40 mm diam), maximum 33/36°C. Colony reverse on OA and PDA yellowish white to pale yellow (4A2–3) in darkness, to pale orange (5A3) in daylight, not pigmented on CMD; after incubation under UV pale to light orange to reddish orange (6A3–4 to 7A5–6) on all media. Colony surface on OA finely felty because of the sparsely produced aerial mycelium, granulose because of conidial masses, or smooth when sterile; on PDA forming abundant aerial mycelium arranged as hyphal strands, sporulation absent or sparse. **Conidiophores** dimorphic. Primary conidiophores verticillium-like, inconspicuous, sometimes absent. Secondary conidiophores penicillate, mononematous or weakly sporodochial; phialides cylindrical, to 40 µm long, around 2.0 µm wide at base and near aperture, without a visible collarette; secondary conidiophores penicillate conidiophores terverticillate or more highly-verticillate, or irregularly branched, with phialides also arising from lower levels; phialides in apical whorls of 2–5, also arising from lower levels, narrowly flask-shaped, with widest point in the lower third, slightly and continuously tapering toward the tip, without a visible collarette, (7–)11.2–15.4–18.6(–24.0) µm long, (2–)2.2–2.4–2.6(–3.2) µm wide at base, (2–)3–3.4–3.8(–4.2) µm at widest point, (1.0)1.4–1.6–1.8(–2.2) µm wide near aperture (n = 38). **Conidial masses** whitish to light orange, slimy, on aggregated secondary conidiophores in dome-shaped masses, watery on primary conidiophores. **Conidia** hyaline, curved, apex slightly tapering, slightly laterally protruding, with a laterally displaced hilum, (6.0–)11.2–13–15(–20.2) × (3.2–)4.6–5–5.4(–7) µm (n = 189). Perithecia not observed in culture.

Type for *Nectria apocyni*: U.S.A. NEW YORK: North Greenbush; on lower part of stems of Indian hemp, *Apocynum cannabinum* L.; Oct 1872; C.H. Peck (NY; isotype, N. 4). **Type for *Dendrodochium macrosporum*:** U.S.A. NEW JERSEY: Newfield; on dead herbaceous stem; Nov 1881; J.B. Ellis (PAD, Ellis 3537; ex-type slide no. 129, herb. CBS).

Known distribution: Neotropics (Colombia, Venezuela, French Guiana, Peru), Indonesia, and temperate North America (U.S.A.: New York, New Jersey).

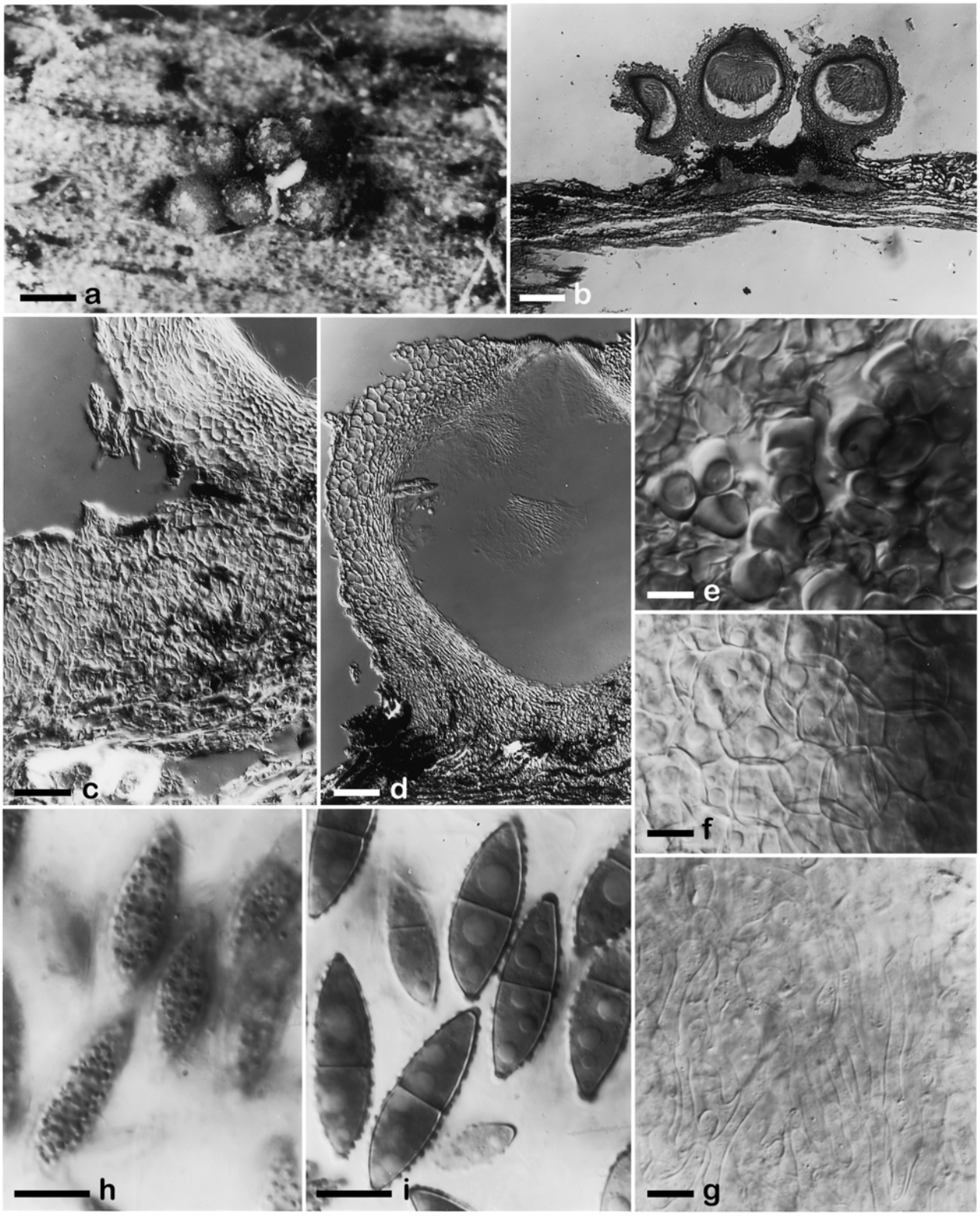


Fig. 8. ***Bionectria apocyni*****. a.** Habit of few, crowded perithecia. **b–d.** Sections through perithecia (b, d), superficial to somewhat erumpent stroma (c), or lateral perithecial wall (d). **e–g.** Surface- or subsurface views of perithecium wall; cells of warts with unevenly thickened walls (e); cells of outer perithecial wall region (f); middle perithecial wall region (g, only observed in few specimens). **h, i.** Discharged ascospores, surface view (h) and optical section (i). – a: Dumont-CO 9531; b: type; c, d: Dumont-CO 5053; e: Dumont-VE 1417; f: Dumont-CO 5052; g: Dumont-CO 3569; h, i: Dumont-CO 5347. All from natural substratum. The section in b was prepared by G.J. Samuels. a: DM; b: LM; others: DIC; h, i stained in cotton blue. Scale bars: a = 300 µm; b = 100 µm; c = 30 µm; d = 50 µm; e–i = 10 µm.

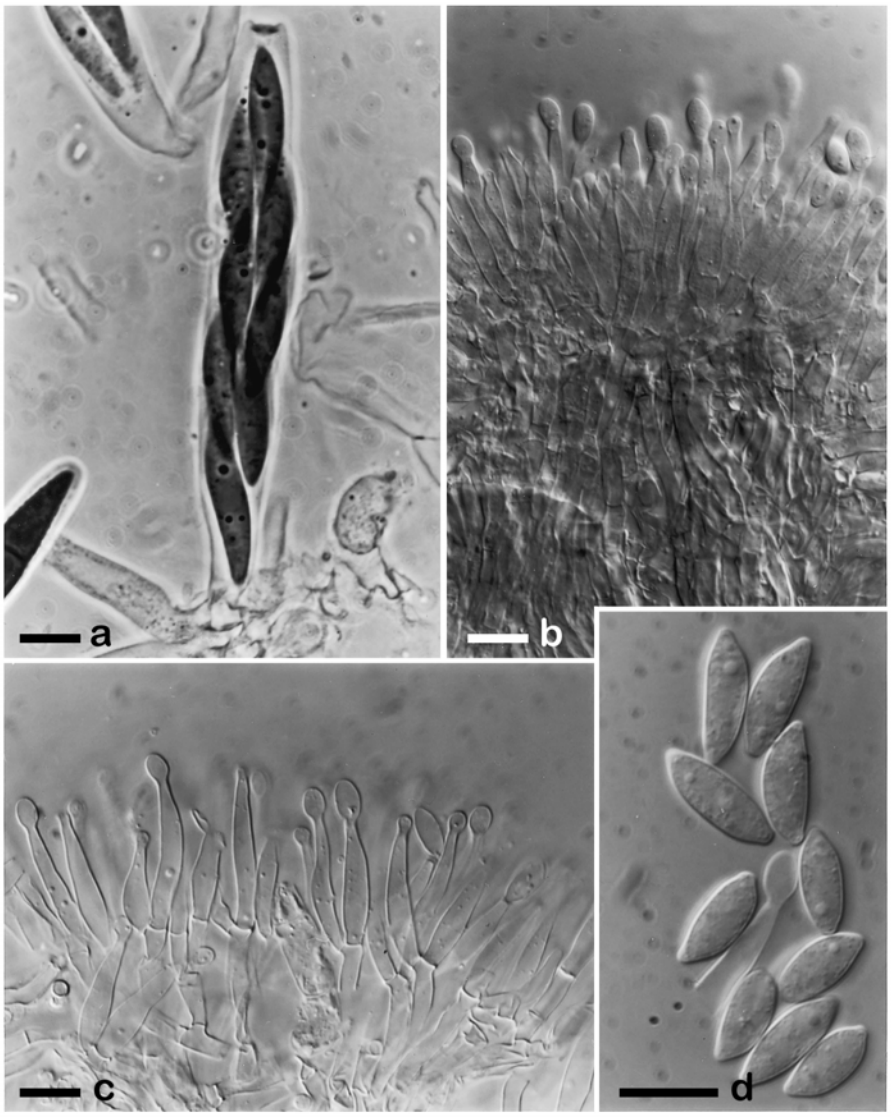


Fig. 9. ***Bionectria apocyni*** **/** ***Clonostachys macrospora*****. a.** Immature ascus, stained with cotton blue, showing ascal ring and cymbiform ascospores. **b, c.** Sections through sporodochium; phialides narrowly flask-shaped, gradually tapering towards the tip. **d.** Conidia, relatively large, slightly curved, with somewhat protruding apex and laterally displaced hilum. – All from natural substratum. a: Dumont-CO 5053; b: CO 7205; c, d: CO 9407. a: PC; b–d: DIC. Scale bars = 10 μm.

Habitat: On bark of recently dead woody plants (particularly from neotropical regions), or on stems of herbaceous plants (commonly on *Apocynum cannabinum*).

Published description and illustration: Samuels (1976a), Schroers & Samuels (1997).

Additional specimens/strains examined: COLOMBIA. Dpto. Boyacá: Along the Sogamoso–Aguazul Rd., *ca* 38 km from intersection with Sogamoso–Aquitania Rd., *ca* 3000 m alt.; on *Chusquea* culm; 13 Jan 1976; K.P.D., S.E. Carpenter, M.A. Sherwood, L.A. Molina (NY; Dumont-CO 5052; Dumont-CO 5053). – *Ca* 64 km from Aguazul, on the Aguazul–Sogamoso Rd., *ca* 1700 m alt.; on indet. branch; 14 Jun. 1976; K.P.D., S.E. Carpenter, M.A. Sherwood, L.A. Molina (NY; Dumont-CO 5347). – Dpto. Cundinamarca: Between km posts 29–30 from Zipaquirá, on the Zipaquirá–Pacho Rd., *ca* 3300 m alt.; on unidentified herbaceous stem; 9 Jun 1976; K.P.D., S.E. Carpenter, M.A. Sherwood, L.A. Molina (NY; Dumont-CO 4484). – Páramo Cruz Verde, 20 km E of Bogotá, 3000 m alt.; on branch; 4 Jul 1978; K.P.D., L. Ryvarden, F. Oberwinkler (NY; Dumont-CO 9407). – Dpto. Nariño: Vic. km posts 122–123 from Pasto on the Pasto–Tumaco Rd., *ca* 1330 m alt.; on undetermined monocotyledonous stem; 30 Jan 1976; K.P.D., P. Buriticá, L.A. Molina, J.L. Luteyn (NY; Dumont-CO 3929). – Road between Pasto and Sibundoy at km 44, 6 km before Santiago, *ca* 2400 m alt.; on branch; 7 Jul 1978; K.P.D., F. Oberwinkler, M. Pulido (NY; Dumont-CO 9531; Dumont-CO 9532; Dumont-CO 9533). – Vic. km posts 13–14 from Pasto on the Pasto–Mocoa Rd., 3500 m alt.; K.P.D., P. Buriticá, J.L. Luteyn, L.A. Molina; on unidentified bamboo; 25 Jan 1976 (NY; Dumont-CO 3500). – Vic. km posts 44–45 from Pasto on the Pasto–Mocoa Rd., Intendencia Putumayo, *ca* 3000 m alt.; on unidentified stem; 25 Jan 1976; K.P.D., P. Buriticá, L.A. Molina, J.L. Luteyn (NY; Dumont-CO 3569). – Dpto. Magdalena: Sierra Nevada de Santa Marta, between Palo Alto (1700 m) and Refugios de la Sierra (1850 m); on branch; 19 Jun 1978; K.P.D., L. Ryvarden, F. Oberwinkler, P. Buriticá, M. Pulido, J. Aguirre (NY; Dumont-CO 8969). – Dpto. Valle del Cauca: *Ca* 60 km from Ansermanuevo, on the Ansermanuevo–San José del Palmar Rd., *ca* 1990 m alt.; on unidentified herbaceous stem; 25 Aug 1976; K.P.D., L.A. Molina, E. Forero (NY; Dumont-CO 7205). – ECUADOR. Prov. Pichincha: *Ca* 39 km SW of Chillogallo, on old road from Quito to Santo, *ca*

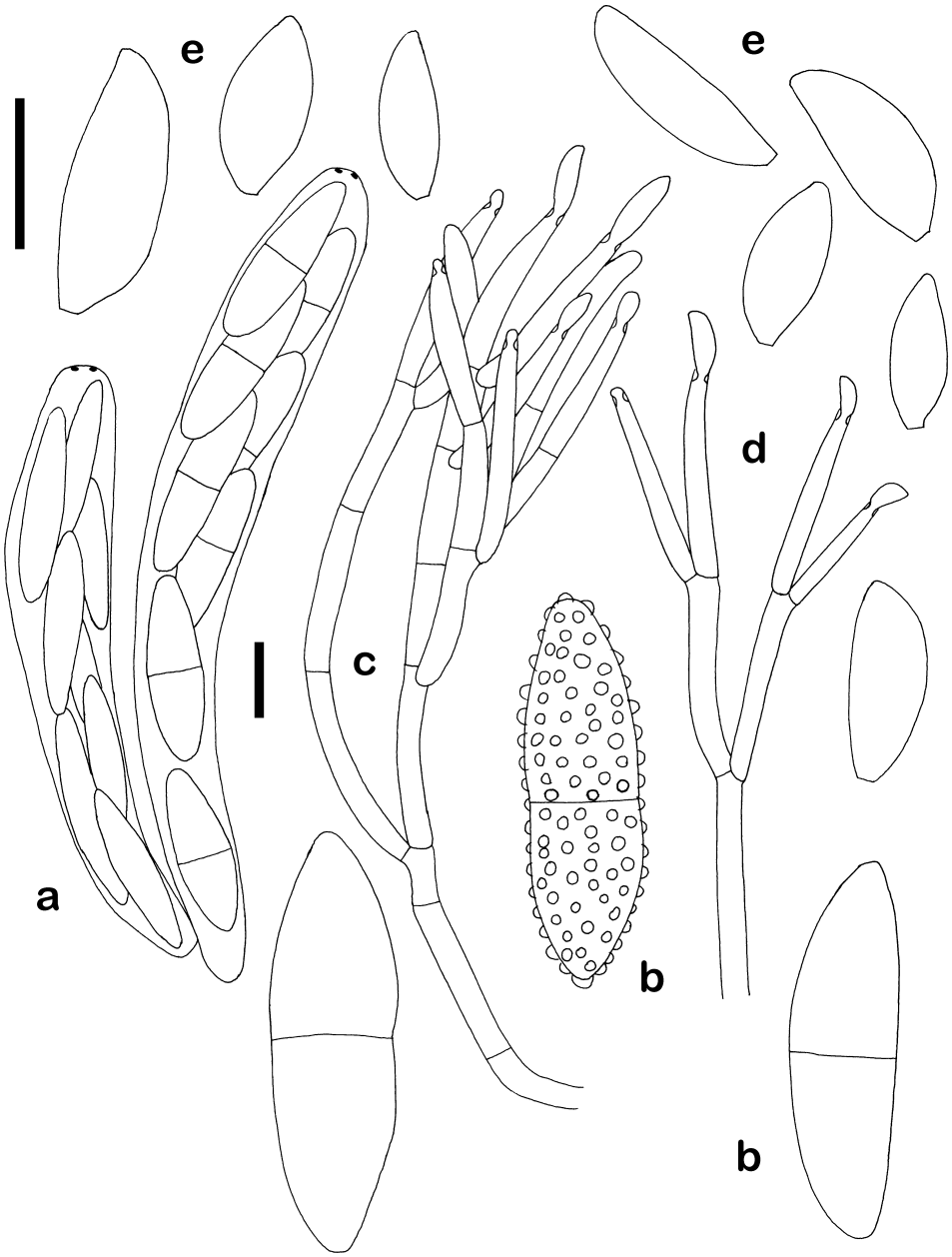


Fig. 10. ***Bionectria apocyni* / *Clonostachys macrospora*. a.** Immature and almost mature ascus, apical ring almost invisible. **b.** Ascospores. **c.** Conidiophore from young sporodochial pustule. **d.** Verticillium-like conidiophore. **e.** Conidia from tropical (left) and temperate specimen (right). – a, b: natural substratum; c–e (right): 7–10-d-old OA culture; e (left): dried culture. a: Dumont-CO 9533; b: Dumont-CO 5347, Dumont-CO 9407; Dumont-CO 5053; c, d: CBS 212.93; e: Dumont-VE 1417 (left), CBS 360.78 (right). Scale bars = 10 μm; the shorter bar applies to a, c, d, the longer to b, e.

2400 m alt.; on twig of unidentified herbaceous stem; 17 Jul 1975; K.P.D., S.E. Carpenter, P. Buriticá (NY; Dumont-EC 200, Dumont-EC 261). – *Ca* 2 km from Puyo, on the Ambato–Puyo Rd., Prov. Pataza, *ca* 1330 m alt.; on undetermined wood; 24 Jul 1975; K.P.D., S.E. Carpenter, P. Buriticá (NY; Dumont-EC 1440); identified as *Nectria rugispora* Pat.). – FRENCH GUIANA. Saint Laurent, Piste Balate, 12 km from Saint Laurent, 54°03' N, 50°23' W, 20 m alt.; on base of *Cecropia* petiole; 19 Nov 1986; A.Y. Rossman, C. Feuillet, L. Skog (NY; A.Y.R. 4056; Rossman culture 4056). – U.S.A. NEW YORK: Bronx Co., The New York Botanical Garden; on dead stem of *Apocynum cannabinum*; 17 Oct 1986; G.J.S., C.T.R. (NY; G.J.S. 86-552; specimen and culture, anamorph only; CBS 130.87, CBS 212.93). – The New York Botanical Garden, south of meadow; on dead stem of *Apocynum cannabinum*; 1 Dec 1979; C.T.R. (NY; 79-329A; C.T.R. isolate 79-329A, perithecia immature, anamorph present). – The New York Botanical Garden, south of meadow; on dead stems of *Apocynum cannabinum*; 29 Oct 1980; C.T.R. (NY; 80-162; C.T.R. isolate 80-162, dead, anamorph only). – PENNSYLVANIA: Chester Co., Kennett Square; on dead stem of *Solidago canadensis* associated with *Nectria* sp.; 6 Nov 1977; C.T.R. (C.T.R. isolate 77-316; CBS 360.78). – VENEZUELA. Edo. Aragua: Ravine, 3.9 km S of Rancho Grande, Parque Nac. Henry Pittier, on Rancho Grande–Maracay Rd.; on unidentified wood; 5 Jul 1971; K.P.D., J.H. Haines, G.J.S. (VEN, NY; Dumont-VE 1417; C.T.R. isolate 71-230 (?=71-240), ?dead). – Edo. Mérida: Laguna Negra, E of Laguna Mucubaji, Parque Nac. Sierra Nevada, near Apartaderos; on unidentified thin ?monocotyledonous bark; 18 Jul 1971; K.P.D., J.H. Haines, G.J.S., A. Revas (VEN, NY; Dumont-VE 2341). – El Teleférico, above Mérida; on unidentified wood; 30 Jul 1971; K.P.D., G.J.S.

(NY; Dumont-VE 3418). – Vic. of El Bachiller, *ca* 19 km W of point where Río Cupira crosses Route 9, between Caracas and Cumana; on unidentified bark; 5 Jul 1972; K.P.D., G.J.S., R.F. Cain, G. Morillo (NY; Dumont-VE 3968). – Edo. Barinas: Ravine, *ca* 68 km N & W of Barracas, on Mérida–Barimas Rd.; on *Rubus* sp.; 26 Jul 1971; K.P.D., G.J.S., L. Borjas (NY; Dumont-VE 3152). – Edo. Sucre: Along Río Aguas Calientes, 30 min walk N of Maraval, NW of Irapa; on unidentified bark; 8 Jul 1972; K.P.D., R.F. Cain, G.J.S., G. Morillo, A. Villegas (VEN, NY; Dumont-VE 4359; C.T.R. isolate 72-79). – Edo. Trujillo: Parque Nacional Guaramacal, on road between Bocono and Guaramacal, 8.4 km from the Batatal–Bocono Rd., 09°15' N, 70°13' W, 2350 m alt.; on woody wine; 22 Nov 1990; G.J.S., B. Hein, S.M. Huhndorf (BG, B, BPI, USB, VEN, NY; G.J.S. 7392).

Notes: *Bionectria apocyni* is characterized by relatively large and coarsely warted ascospores that are oblong-ellipsoidal to cymbiform and 1-septate (Figs 8 h, i; 10 b). Some ascospores of some specimens were 2- or 3-septate after discharge, as in *B. tonduzii*. Based on the shape and size of the ascospores, perithecial wall anatomy, and associated anamorphs, a large number of tropical collections on bark were identified as *B. apocyni*, in addition to a few temperate specimens. The species is also characterized by rather large and wide conidia (Figs 9 d, 10 e).

The anamorph of *B. apocyni* is confirmed at least for some tropical specimens although only dried colonies of ascospore isolates were available (e.g. Dumont-VE 4359, Dumont-VE 1417). No confirmed ascospore isolates from the type location (U.S.A.: New York) or other temperate regions could be studied. In addition to the similar morphology, perithecia from both tropical and temperate regions are sometimes associated with sporodochia that all form conidia of the same shape and a similar size range, which is characteristic for *B. apocyni*/*C. macrospora* and *B. tonduzii*. The sporodochia frequently are small, slightly higher than wide and widening in the upper parts; they differ in this respect from the robust sporodochia formed in most other species of *Bionectria*. The conidia are typical of subgenus *Bionectria* (slightly curved, hilum laterally displaced) but differ from those of most other species in a somewhat tapering distal ends. The interpretation of *D. roseomucosum* as a synonym of *D. macrosporum* is based on its characteristic conidial size and shape and penicillate conidiophores (Matsushima, 1995: Pl. 18, Fig. 829, 830). The most similar species are *B. oblongispora* (conidia shorter, more slender, and with a more rounded distal end, Fig. 12 e), and *B. kowhaii* (conidia ± straight, frequently widest in the lower third, Figs 14 d, 15 d). Segregation of these species also corresponds with differences in the morphology and size ranges of ascospores. A few neotropical collections previously identified as *N. apocyni* were redetermined as *B. oblongispora* based on their slender conidia (observed from the natural substratum) and shorter ascospores.

3. Bionectria oblongispora Schroers, *sp. nov.* — Figs 11 a–f, 12 a, b.

Anamorph: ***Clonostachys oblongispora*** Schroers, *stat. nov.* — Fig. 12 c–e.

Bionectriae byssicolae similis sed conidiis longioribus, (16–)16.8–17.6–18.2(–20) × (4.2–)4.8–5–5.4(–5.8) µm. *Bionectriae apocyni* similis sed ascosporis minoribus angustioribusque, (9–)12.6–13.6–14(–19.8) × (2.6–)3.2–3.6–3.8(–4.2) µm, conidiis angustioribus, apice rotundatis.

Holotypus teleomorphosis: BPI 748343. Holotypus anamorphosis: BPI; cultura sicca, isolata ex specimine BPI 748343; isotypus herb. CBS; cultura viva CBS 100285.

Etymology: *Oblongisporus*, referring to the relatively long conidia.

Description from natural substratum: Stroma well-developed, erumpent through bark; cells angular to subglobose, pseudoparenchymatous, vacuolate, becoming prosenchymatous towards the base. **Perithecia** crowded on the stroma in groups of up to 50, subglobose, 250–300(–350) µm diam, slightly pinched laterally or not pinched when dry, light orange, ostiolar region slightly deeper orange, with a scaly to warted surface. **Perithecial warts** to 70 µm high, to 100 µm diam, whitish or off-white; cells angular to globose, with unevenly thickened walls up to 9 µm thick, intergrading with the cells of the outer perithecial wall region. **Perithecial wall** *ca* 45 µm thick, consisting of three regions. Outer region *ca* 25 µm or to 4 cells thick; cells angular to globose, 6–15 × 5–10 µm, with uniformly thickened walls up to 2 µm thick, with orange vacuoles. Middle region inconspicuous, 5–10 µm thick, consisting of one or two layers of intertwined hyphae. Inner region *ca* 15 µm thick. **Asci** narrowly clavate, 68–80 × 9–14 µm (n = 6), 8-spored; apex narrowly rounded, ring inconspicuous, flat. **Ascospores** ellipsoidal to broadly ellipsoidal, slightly tapering towards the ends, spinulose, colourless, (16–)16.8–17.6–18.2(–20) × (4.2–)4.8–5–5.4(–5.8) µm (n = 32). **Sterile mycelium** and sporodochia not seen.

Description from culture: Colonies reaching 25–35 mm diam in 7 d at 24ºC; optimum for growth 24°C (35 mm diam), maximum 27°C. Colony reverse pale yellow to pale orange (4–5A2), also when incubated under UV. Colony surface on OA felty to cottony, finely to coarsely granular, pale orange (5–6A2–3) because of somewhat sporodochial or confluent conidial masses; aerial mycelium sparsely developed; on CMD similar but sporulation and mycelium less developed. **Conidiophores** weakly dimorphic. Primary conidiophores verticillium-like, with long stipes, mono- to biverticillate; phialides adpressed or divergent; secondary conidiophores arranged in pustules or sporodo-

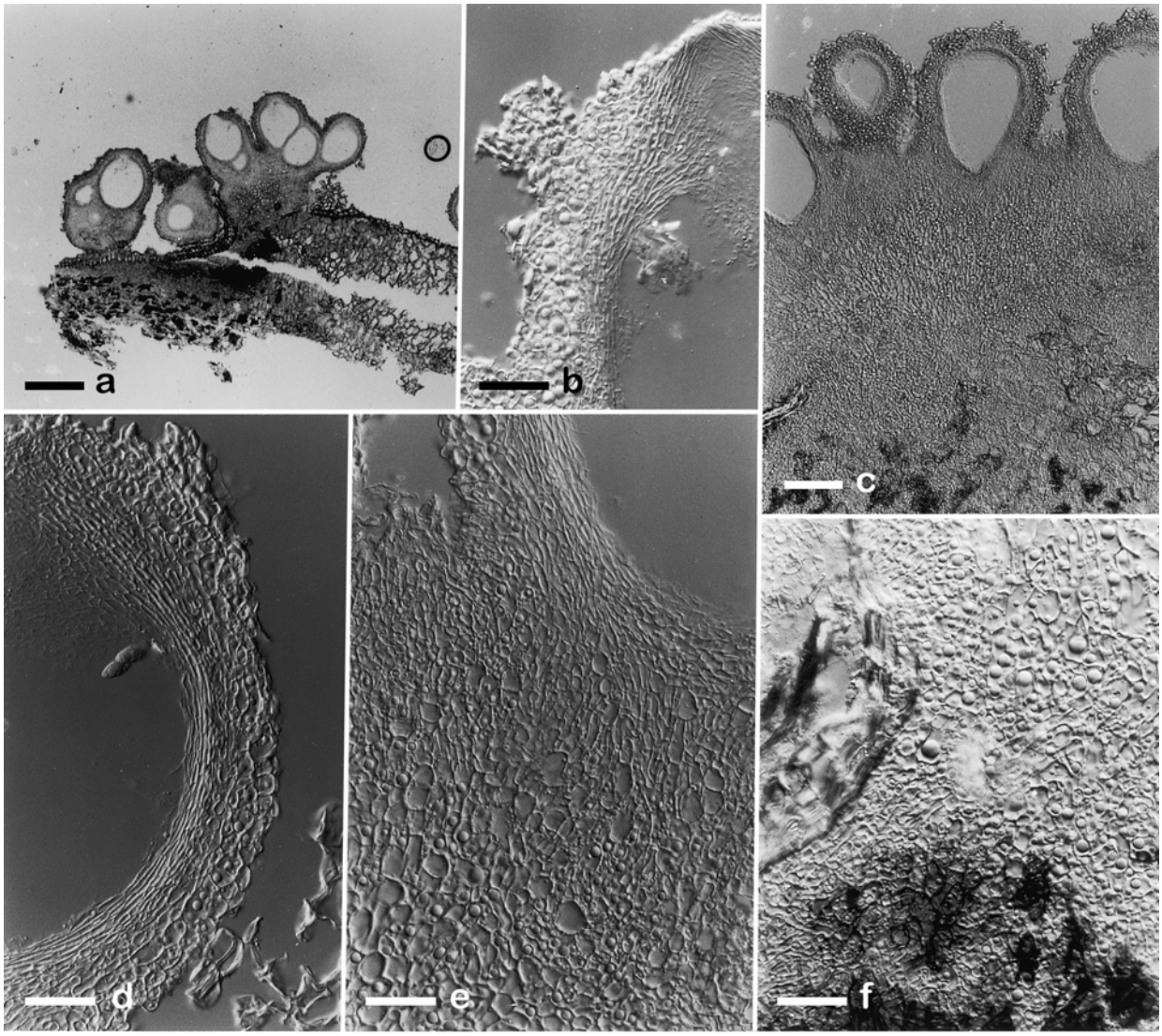


Fig. 11. ***Bionectria oblongispora*****. a–f.** Sections through perithecia and stroma. **a.** Perithecia crowded on stroma. **b.** Upper part of perithecium with small wart. **c.** Perithecial stroma. **d.** Lateral perithecial wall. **e.** Stroma near base of perithecium. **f.** Angular cells of subcortical stroma containing droplets. – All from natural substratum, BPI 748343. a: LM; b–f: DIC. Scale bars: a = 250 µm; b, d–f = 30 µm; c = 100 µm.

chial, to quinquies-verticillate, branches and phialides more or less divergent or cylindrical and hardly tapering towards the tip, without a visible collarette, (11.8–) 13.2–18.2–20.4(–38) µm almost adpressed; phialides narrowly flask-shaped, with widest point in the lower third or almost long, (2.6–)2.6–3–3.2(–3.8) µm wide at base, (2.6–) 3.2–3.2–3.4(–3.8) µm at widest point, (1–) 1.4–1.4–1.6(–1.6) µm wide near aperture (n = 33). **Conidial masses** light orange, particularly when incubated in daylight, slimy, consisting of imbricate conidial chains, later confluent to masses over several conidiophores. **Conidia** ellipsoidal to oblong-ellipsoidal, with one side almost straight and the other slightly curved, with a rather rounded distal end, with a slightly laterally displaced, not protruding hilum, (9–)2.6–13.6–14(–19.8) × (2.6–)3.2–3.6–3.8(–4.2) µm (n = 32). **Sporodochia** only observed as old remnants seated on some of the perithecial clusters of specimen D-317.

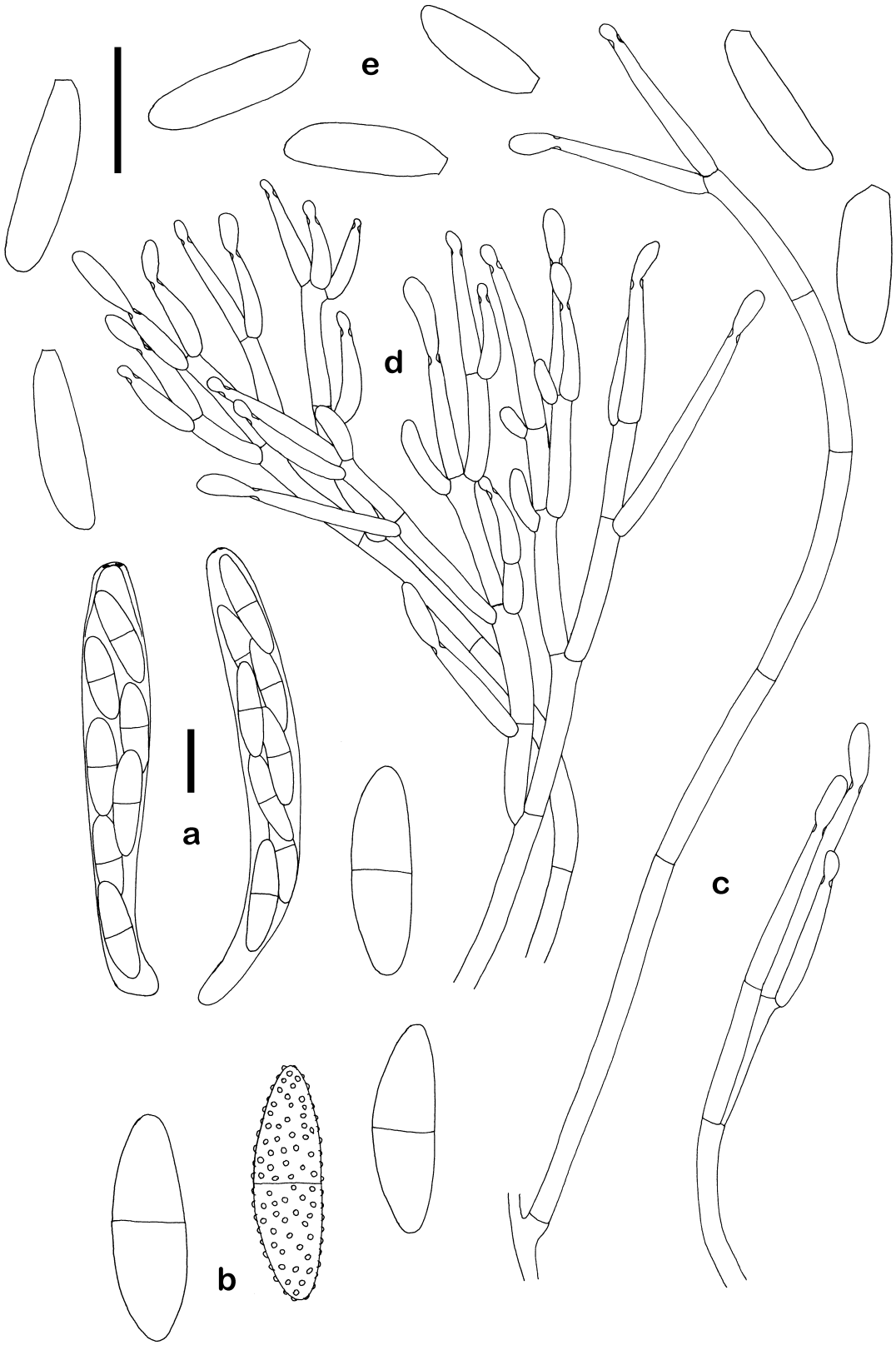


Fig. 12. ***Bionectria oblongispora*** **/** ***Clonostachys oblongispora*****. a.** Almost mature asci with inconspicuous apical ring. **b.** Discharged ascospores. **c.** Solitary, little-branched primary conidiophores. **d.** Much-branched secondary conidiophores from sporodochial pustule. **e.** Conidia, ellipsoidal with one flattened side, ± rounded apex and laterally displaced hilum. – All from CBS 100285 (BPI 748343): 10-d-old OA culture. Scale bars = 10 µm; the shorter bar applies to a, c, d, the longer to b, e.

Type for *Bionectria oblongispora*: JAPAN. Kakuma valley, Sanada-Town, Nagano Prefecture, 1036 m alt.; on bark of trunk of a dying tree of *Orixa japonica* Thunb., together with *Tympanosporium* sp. growing on the perithecia; 13 Aug 1997; H.-J. Schroers 0206, S. Tokumasu, W. Gams, M. Klamer, T. Gräfenhan (BPI 748343; ex-type strain: CBS 100285, derived from ascospores of BPI 748343). **Type for *Clonostachys oblongispora*:** dried culture ex CBS 100285, filed together with BPI 748343; isotype: herb. CBS.

Known distribution: Japan, ?neotropical.

Habitat: Bark of a dead part of standing and still living *Orixa japonica* Thunb.

Additional specimens examined: COLOMBIA. Dpto. Cundinamarca: El Bosque de Tibabita, E. Jardines de Paz; on stem of *Chusquea* sp.; 28 Jun 1974; K.P.D., J.H. Haines, J.M. Idrobo, L.F. Velásquez (NY; Dumont-CO 15). – JAPAN. Iwate Pref.: Odagoe, foot of Mt. Ha-yachine; on bark; 18 Jul 1967; Y. Doi (NY, ex TNS; D-317). U.S.A. HAWAII: Oahu, Kauai, Awaawapuhi trail, Kokee St. Park.; on branch of fallen tree; 21 Nov 1985; S.E. Carpenter (NY; Carpenter 35).

Notes: *Bionectria oblongispora* is similar to *B. byssicola* in morphology of the ascospores (dimension of warts and measurements) and perithecium morphology. Conidia in *B. oblongispora* are longer than generally observed in species related to *B. ochroleuca* and fall in the size range of *B. apocyni*, *B. tonduzii*, and *B. kowhaii*. The conidia, however, are oblong-ellipsoidal, only slightly curved, rather narrow, and have a rounded distal end, while the hilum is clearly laterally displaced. The conidia thus differ from those of *B. apocyni* (more curved, distal end tapering) and *B. kowhaii* (broader, frequently obclavate, often mostly straight). The species differ in perithecial wall thickness, which is less than 50 µm in *B. oblongispora* and generally more than 50 µm in *B. apocyni* and *B. kowhaii*. Comparable characters of ascospores and conidia have been observed in two additional neotropical specimens, formerly identified as *B. apocyni*, and in one specimen from Japan, however, those of the anamorph could not be confirmed in cultures of ex ascospore isolates. The type specimen of *B. oblongispora* was collected from dead parts of a still living tree, which is unusual for *Bionectria*. The perithecia were parasitized by *Tympanosporium* sp. (CBS 100286, in mixed culture with *B. oblongispora*), but no fungus was observed parasitized by *B. oblongispora*. The possibility that *B. oblongispora* is plant-parasitic cannot be excluded.

4. Bionectria kowhaii (Dingley) Schroers, *comb. nov.* — Figs 13 a–j, 14 a, 15 a, b.

≡ *Nectria kowhaii* Dingley, Trans. Roy. Soc. New Zealand 83: 654. 1956 (as '*kowhai*').

Anamorph: ***Clonostachys kowhaii*** Schroers, *stat. nov.* — Figs 14 b–d, 15 c, d.

Conidiophora dimorphica, phialides ad apicem ad 3 µm latae. Conidia quasi recta vel minute curvata, saepe latissima in parte inferiore, obclavata, sursum ad apicem exigue rotundatum angustata, hilo symmetrico vel paulo laterali, applanato vel inconspicuo neque protrudente praedita, (4.4–)7.6–10.6–13.2(–18.2) × (2.8–)3.4–4–4.6(–5.8) µm.

Holotypus anamorphosis: BPI; cultura sicca, isolata ex specimine BPI 748345 (G.J.S. 95-4); isotypus herb. CBS; cultura viva CBS 461.95.

Description from natural substratum: Stroma well-developed, erumpent through bark, bearing sporodochia or perithecia, sometimes close to the black stroma of other pyrenomyetes; cells angular to subglobose, pseudoparenchymatous, becoming prosenchymatous towards the stromal base. **Perithecia** crowded in small groups of < 10–30, globose to subglobose, 300–450 µm high, 300–600 diam, apically slightly pinched or not pinched when dry, light orange, brownish with age, not papillate, ostiolar region in dried condition slightly sunken, not markedly contrasting with the perithecial wall, with a scaly to warted surface. **Perithecial warts** *ca* 30–60 µm high, 40–100 µm diam, whitish or off-white; cells angular to globose, with evenly thickened walls up to 2 µm thick or with unevenly thickened walls up to 8 µm thick. **Perithecial wall** 60–90 µm thick, consisting of three regions. Outer region 30–45 µm or to 5 cells thick; cells angular to globose, 8–22 × 5–18 µm, with uniformly thickened walls up to 2 µm thick, with orange to somewhat red vacuoles. Middle region 10–16 µm thick, consisting of few layers of intertwined hyphae. Inner region 15–30 µm thick. **Asci** narrowly clavate, 75–110 × 10–17.5 µm (n = 28), 8-spored or less than 8-spored; apex rather broadly rounded, ring inconspicuous, flat. **Ascospores** ellipsoidal to broadly ellipsoidal, slightly tapering towards the ends, rough to somewhat warted, colourless, (14.6–)16.6–18.2–19.6(–23.2) × (5–)5.8–6.4–7(–8.4) µm (n = 80); discharged ascospores sometimes with an additional septum (3- celled). **Sterile mycelium** not conspicuous on the substratum. **Sporodochia** *ca* 500 µm diam, consisting of densely packed subhymenial hyphae forming a *textura porrecta* in longitudinal section; hyphae running subcortically under the surface of the bark continuous with the base of the erumpent sporodochium/perithecium-cluster; conidia slightly curved to ellipsoidal, with a laterally displaced hilum, 13.5–25.0 × 4.5–5.5 µm.

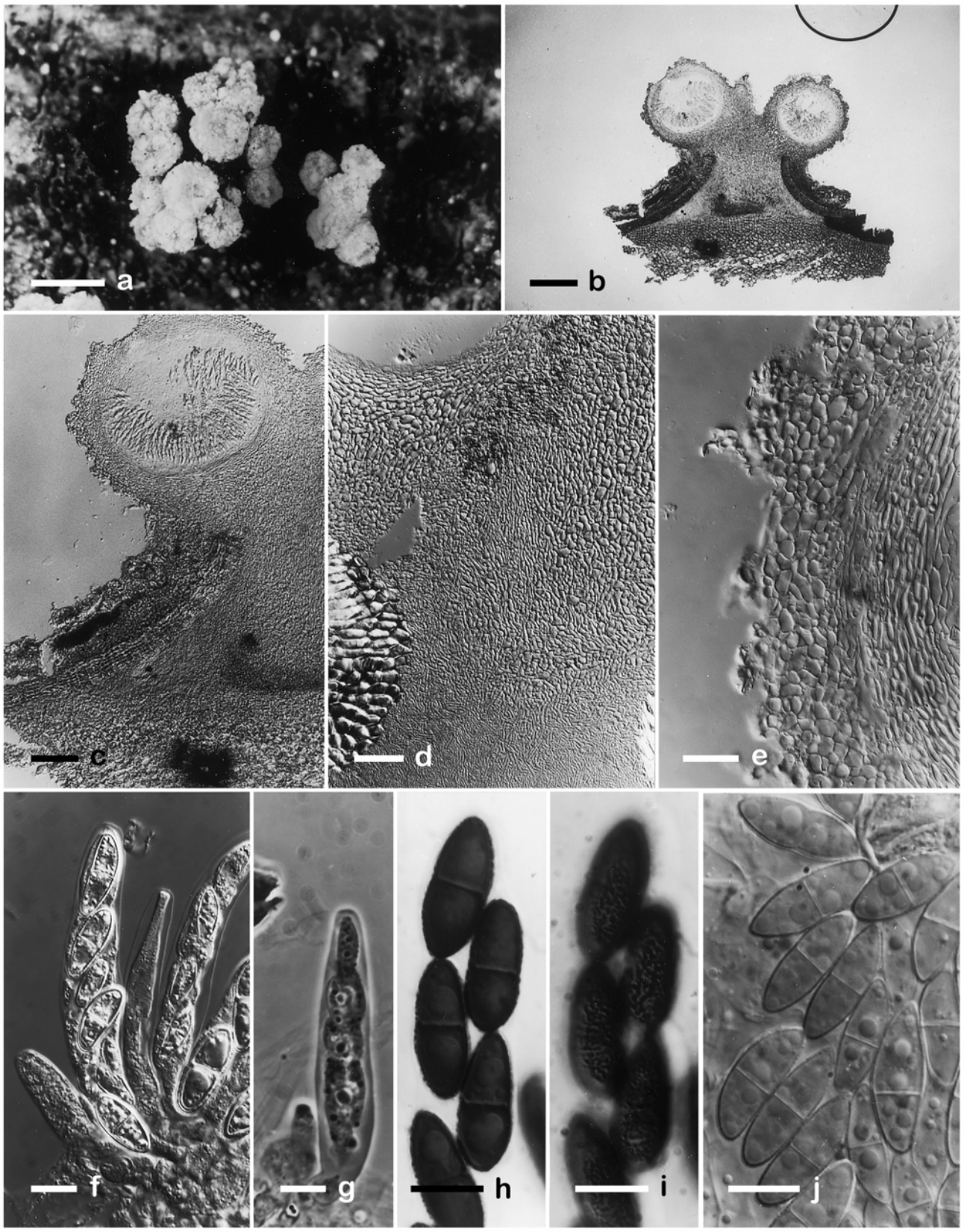


Fig. 13. ***Bionectria kowhaii.*** **a.** Habit of crowded perithecia. **b–e.** Sections through perithecia and stroma; pseudoparenchymatous cells of stroma, becoming prosenchymatous subcortically (c, d); lateral perithecial wall showing three regions (e). **f, g.** Almost mature (f) and immature (g) asci; ring hardly visible. **h, i.** Ascospores of mature ascus in optical section (h) and surface view, finely warted (i), stained with cotton blue. **j.** Discharged ascospores in optical section. a, d, e, g, j: BPI 748345 (CBS 461.95); b, c: PDD 12800; f, h, i: PDD 31796. – All from natural substratum. a: DM; b: LM; c–f, h–j: DIC; g: PC. Scale bars: a = 500 µm; b = 250 µm; c = 100 µm; d = 50 µm; e = 30 µm; f–j = 10 µm.

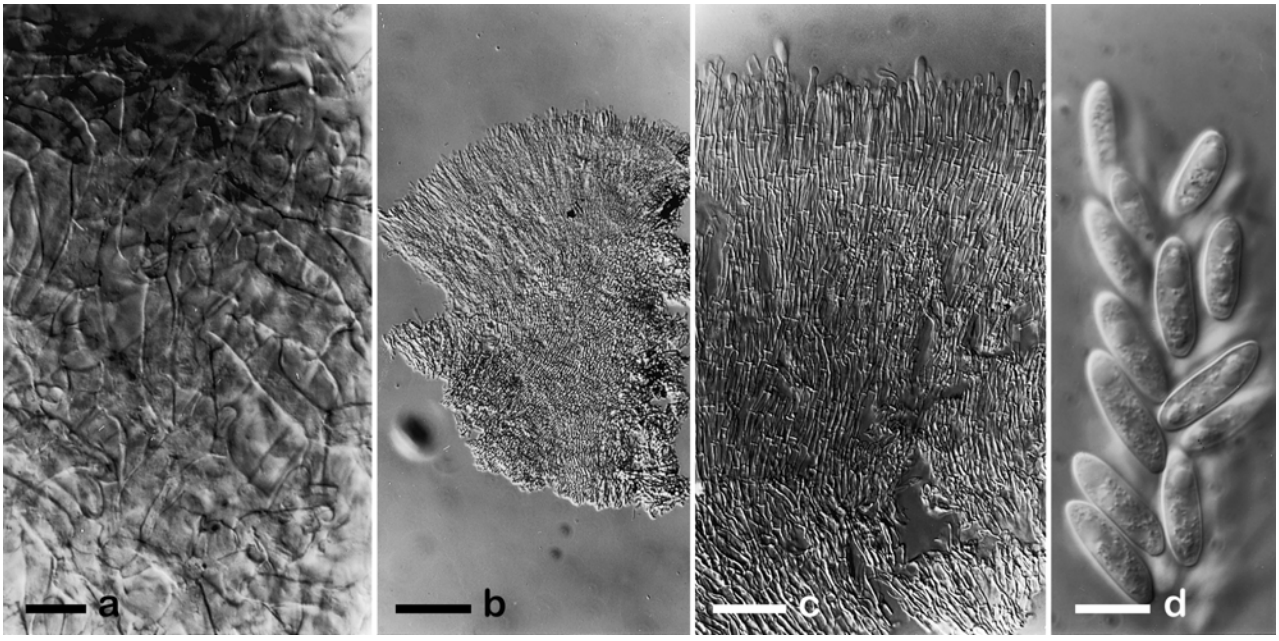


Fig. 14. ***Bionectria kowhaii* / *Clonostachys kowhaii*. a.** Subsurface view of middle perithecial wall region. **b, c.** Sections through sporodochia. **d.** Imbricate conidia. – All from G.J.S. 95-4 (CBS 461.95). a–c: natural substratum; d: dried culture. a, c, d: DIC; b: LM. Scale bars: a = 10 µm; b = 100 µm; c = 30 µm; d = 10 µm.

Description from culture: Colonies reaching *ca* 8 mm in 7 d at 24ºC; optimum for growth 18–21°C (15 mm diam), maximum 27°C. Colony reverse pale to light orange (5–6A2–4); pigmentation and growth less developed under UV. Colony surface on OA finely to coarsely granular, pale orange because of the conidial masses; aerial mycelium sparsely developed; on CMD similar but sporulation and mycelium less developed. **Conidiophores** weakly dimorphic. Primary conidiophores sparsely and divergently branched; stipe long, arising from the sparsely developed aerial mycelium; secondary conidiophores penicillate, irregularly quinquies-verticillate, with solitary side-branches arising at several levels along the main axis; stipes short or about the length of the branching part, 40–100 µm long, to 5 µm wide at base; branches and phialides somewhat divergent or almost adpressed; phialides normally formed in whorls of two or solitary, almost cylindrical, hardly tapering towards the tip, or narrowly flask-shaped with widest point in the lower third, with or without a visible collarette, (13.6–)21.8–26.2–28.8 (–42) µm long, (2–)2.2–2.6–2.8(–3.2) µm wide at base, (1.6–)2–2.2–2.4(–3) µm wide near aperture (n = 33). **Conidial masses** light orange, initially in short, relatively thick slimy, imbricate chains, later confluent over several conidiophores. **Conidia** ellipsoidal, straight or minutely curved, sometimes widest in the lower part, tapering towards a narrowly rounded apex (obclavate), with a median or slightly laterally displaced, not protruding, distinctly flat or almost invisible hilum, (4.4–)7.6–10.6–13.2(–18.2) × (2.8–)3.4–4–4.6(–5.8) µm (n = 74). Distinct sporodochia not produced.

Type for *Nectria kowhaii*: NEW ZEALAND. Auckland, Piha Valley; on bark of *Sophora microphylla* Aiton; 15 Aug 1953; J.M. Dingley (PDD 12800). **Type for *Clonostachys kowhaii*:** NEW ZEALAND. Nelson Bays, Lake Rotoroa; on ?*Sophora microphylla*; 18 May 1994; P.R. Johnston [dried culture ex CBS 461.95, derived from ascospores of G.J.S. 95-4 and filed with it in BPI (BPI 748345); isotype: herb. CBS].

Known distribution: New Zealand.

Habitat: On bark of *Sophora microphylla* (vernacular *kowhai*) or *Neopanax* sp.

Published description: Dingley (1956).

Additional specimens/strains examined: NEW ZEALAND. Auckland, Waitemata Co., Waitakere Ranges, vic. Kitekite Stream, along Marguerite Track; on decorticated wood and bark of *Neopanax* sp.; 30 May 1973; J.M. Dingley, G.J.S., S. Haydon (NY ex PDD 31796; G.J.S. 73-92).

Notes: *Bionectria kowhaii* is characterized by relatively large perithecia and relatively large, hardly warted ascospores (Fig. 13 h–j). The ascal ring is reduced, possibly as a consequence of ascospore size (Fig. 13 f, g). Only two specimens that are the same in almost all characters represent the species, which is only known from New Zealand. Perithecial wall anatomy, stroma morphology and the habit of the perithecia are similar to other species of subgenus *Bionectria* (Figs 13 a–e, 14 a). The anamorph is characterized by large conidia of somewhat variable shape (ellipsoidal to obclavate, Figs 14 d, 15 d), almost monomorphic conidiophores, relatively broad phialides, and a

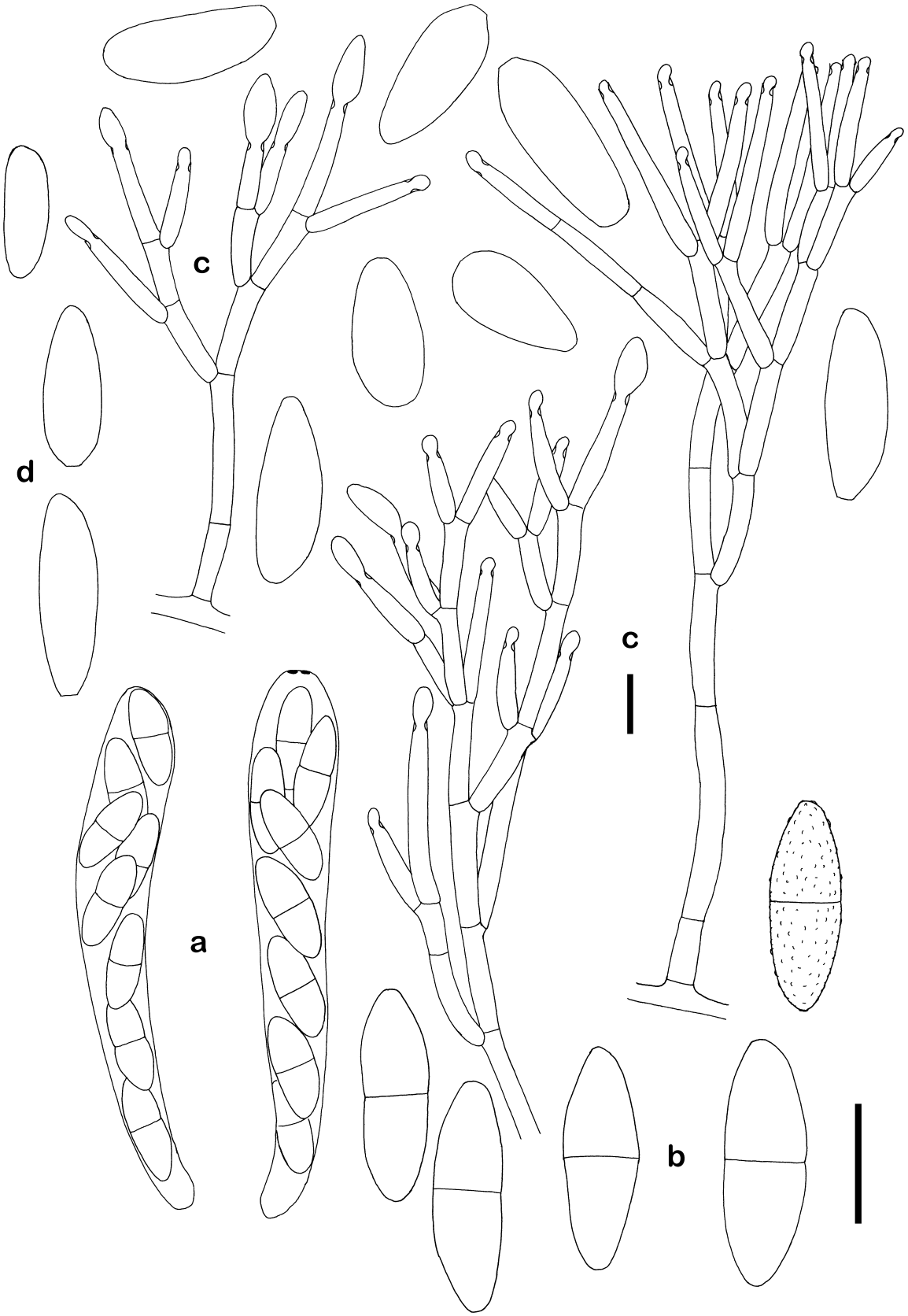


Fig. 15. ***Bionectria kowhaii*** / ***Clonostachys kowhaii*****. a.** Almost mature asci. **b.** Discharged ascospores. **c.** Penicillate conidiophores; solitary side-branches arising in several levels from main axis; phialides almost cylindrical, mostly in pairs; branches and phialides adpressed or somewhat divergent. **d.** Conidia ellipsoidal, almost straight, sometimes obclavate, hilum median or slightly displaced. – a: PDD 12800 (right), G.J.S. 95-4 (left). b: G.J.S. 95-4 (left), PDD 12800 (right); c, d: G.J.S. 95-4. a, b: natural substratum c, d: 14-d-old OA cultures. Scale bars = 10 µm; the shorter bar applies to a, c, the longer to b, d.

rather irregular branching pattern in the conidiophores (Fig. 15 c). Although conidia are generally almost straight, at least part of the conidial population shows a somewhat laterally displaced hilum. As with the sec-

oncary conidiophores of other *Clonostachys* species, conidia aggregate in imbricate chains (Fig. 14 d). Conidiophores are dimorphic, although the verticillium-like (primary) conidiophores are not conspicuously formed. Based on measurements of ascospores and conidia, *B. kowhaii* is similar to *B. apocyni*. The species differ in overall shape of the conidia, ascospore ornamentation (thick-warted in *B. apocyni vs*. small-warted to rough in B. *kowhaii*), a more indistinct or absent middle wall region in *B. apocyni*, and growth rates in culture. The conidial measurements given in the original description, 5–8.5 × 2–3.5 µm (Dingley, 1956), differ considerably from the measurements presented here. No ex-type strain or dried culture, however, was available to verify the original observations, and no strain- or culture number is given in the description. The anamorphic characters presented here are all taken from cultures derived from ascospores of a recent teleomorph collection (CBS 461.95) that in all characters is indistinguishable from the type specimen.

Based on phylogenetic inferences from the *tub*2 gene, *B. kowhaii* is closely related to *B. apocyni* (Figs 3, 4 a–c). They differ, however, by several bp differences resulting in long terminal branches.

5. **Bionectria ochroleuca** (Schw.) Schroers & Samuels, Z. Mykol. 63: 151. 1997. — Fig. 35 d, k; Schroers *et al*., 1999b: Figs 1–6, 8–19.

≡ *Sphaeria ochroleuca* Schw., *Trans. Amer. Philos. Soc*. 2, 4: 204. 1834.
= *Nectria aureofulva* Cooke & Ellis, Grevillea 7: 8. 1878.
≡ *Bionectria aureofulva* (Cooke & Ellis) Schroers & Samuels, Z. Mykol. 63: 153. 1997.
= *Nectria gliocladioides* Smalley & Hansen, Mycologia 49: 533. 1957.

Anamorph: ***Clonostachys rosea*** f. ***rosea***.

Clonostachys rosea (Link : Fr.) Schroers, Samuels, Seifert & W. Gams, Mycologia 91: 369. 1999. f. **rosea**. — Fig. 36 f; Schroers *et al*., 1999b: Figs 7, 20–33.

≡ *Penicillium roseum* Link : Fr., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 7: 37. 1816 (sanctioned by Fries, Syst. mycol. 3: 409. 1832; neotypified in Schroers *et al*., 1999b).
≡ *Gliocladium roseum* (Link) Thom, U.S. Dep. Agric. Bur. Animal Industr. Bull. 118: 49. 1910. [Nom. illeg. Art. 53 (Greuter *et al*., 2000)].
?= *Tubercularia carpogena* Corda, Icones Fungorum 1: 4. 1837 (as '*carpigena*'; PRM).
?= *Clonostachys araucaria* Corda, *Prachtflora*, p. 31. 1839. (iconotype; no type preserved at PRM).
≡ *Stachylidium araucarium* (Corda) Bonorden, Handb. allg. Mykol. p. 110. 1851 (as '*auracarium*'); Pl. 155 *in* Abhandlungen aus dem Gebiete der Mykologie. Zweiter Theil. 1870.
= *Torula rosea* Preuss in Sturm, Deutschl. Fl. 3, fasc. 25, Tab. 7: 13. 1848.
≡ *Oospora rosea* (Preuss) Sacc. & Vogl., Syll. Fung. 4: 18. 1886.
= *Verticillium epimyces* Berk. & Broome, Ann. Mag. Nat. Hist., Ser. 2, 7: 102. 1851.
?= *Clonostachys araucaria* var. *rosea* Preuss, Linnaea 25: 727. 1852.
= *Clonostachys araucaria* var. *compacta* Preuss, Linnaea 25: 727. 1852 (B).
= *Clonostachys populi* Harz, Bull. Soc. Imp. Naturalistes Moscou 44: 116. 1871; Hedwigia 11: 129. 1872 (iconotype).
≡ *Clonostachyopsis populi* (Harz) Höhnel, Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1, 116: 149 (Fragm. Mykol. 3: No. 147: 67). 1907.
= *Verticillium stigmatellum* Berk. & M.A. Curtis, Grevillea 3: 110. 1875.
= *Dendrodochium rubellum* Sacc. var. *macrosporum* Sacc., Michelia 2: 580. 1882.
= *Dendrodochium densipes* Sacc. & Ellis, J. Mycol. 4: 117. 1888.
= *Clonostachys gneti* Oudem., Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch. Ser. 3: 321. 1890 (L).
= *Dendrodochium strictum* D. Sacc., Atti Soc. Ven.-Trent. Sci. Nat. Ser. 2, 2: 478. 1896; Bull. Trimestriel Soc. Mycol. Fr. 12: 80. 1896 (synonymy accepted *fide* W. Gams).
= *Clonostachys populi* var. *aesculi* Oudem., Ned. Kruidk. Arch. Ser. 3, 2: 1121. 1904 (material not located in L).
= *Gliocladium roseum* Bainier, Bull. Trimestriel Soc. Mycol. France 23: 111. 1907.
≡ *Clonostachys araucaria* var. *confusa* Pinkerton, Ann. Missouri Bot. Gard. 23: 44. 1936.
= *Isaria clonostachyoides* Pritchard & Porte, Phytopathology 12: 167. 1922 (R. A. Samson, pers. comm.).
= *Verticillium pulverulentum* Gouwentak, Meded. Phytopathol. Lab. 'Willie Commelin Scholten' 8: 55. 1924.
= *Verticillium foexii* van Beyma, Meded. Phytopathol. Lab. 'Willie Commelin Scholten' 12: 31. 1928.
= *Gliocladium aureum* Rader, Phytopathology 38: 450. 1928.
= *Gliocladium verticillioides* Pidoplichko, Khran. Sakh. Svekly 1: 365. 1930; Fungus flora of coarse fodders: 195. 1953.
= *Gliocladium cholodnyi* Pidopl., Khran. Sakh. Svekly 1: 363. 1930.
= *Verticillium intertextum* Isaac & Davies, Trans. Brit. Mycol. Soc. 38: 155. 1955.

Description from natural substratum (see also Schroers *et al*., 1999): **Stroma** pseudoparenchymatous, erumpent through bark, bearing perithecia mostly in large clusters. **Perithecia** globose to subglobose to oval, 160–250–370 µm high, 150–215–360 µm wide, yellowish orange, light orange, rarely brownish orange, often with a slightly darker contrasting ostiolar region, smooth to rough because of aggregates of small cells. Perithecial wall 25–60 µm thick, composed of three regions. **Asci** narrowly clavate, (41–)49–53–57 (–85) × (4.5–)6.5–7–7.5(–9) µm (n = 140), 8-spored; apex narrowly rounded or flat, with a visible apical ring that often appears triangular in optical section. **Ascospores** ellipsoidal to oblong ellipsoidal, equally two-celled, not constricted or with age slightly constricted at the septum, (7.4–)9.4–10–10.8(–14.4) × (2.2–)3–3.4–3.6(–4.8) µm (n = 684), typically spinulose, rarely smooth, colourless, biseriate above, uniseriate below, almost completely filling the ascus.

Description of cultures of ascospore- and conidial isolates: **Colonies** reaching (25–)35–41–48 mm diam in 7 d at 24ºC; optimum for growth 27ºC [(25–)45–57

Description of cultures of ascospore- and conidial isolates: **Colonies** reaching (25–)35–41–48 mm diam in 7 d at 24ºC; optimum for growth 27ºC [(25–)45–57 mm diam]; maximum 33/36ºC. Colony reverse on OA yellowish white to light yellow, with time orange or with brownish hues, after incubation under UV generally orange-white to light orange or carrot-red; yellow pigment generally diffusing beyond the colony, orange pigment visible only in the agar inside the colony margins; on CMD similar as on OA but colours less intense. Surface mycelium optimally developed on OA, felty to tomentose, arranged in strands particularly towards the colony centre, or granulose because of conidial masses from solitary or aggregated conidiophores. Aerial mycelium on CMD scanty, on PDA strongly developed in thick, often erect hyphal strands. Surface unpigmented, white because of aerial mycelium (PDA) and white conidial masses, or in yellow or orange hues, because of the pigmentation of the agar (CMD, OA), or with yellowish white to orange-white granules because of the conidial masses. **Conidiophores** dimorphic. Primary conidiophores verticilliumlike, formed throughout the colony, dominating towards the margin, arising from the agar surface; stipes (25–)70–200 µm long, 3.5–5.5 µm wide at base, generally longer than the 30–120 µm high branching part, with short side branches arising from the upper part, rarely from the lower part; phialides divergent, in whorls of 2–5, or singly from lower levels, straight, generally slightly tapering towards the tip, with or without a visible collarette, (16.6–)22.8–27.8–31.2 (–46.6) µm long, (1.6–)2.2–2.4–2.6(–3.4) µm wide at base, (1–)1.4–1.6–1.6(–2.4) µm wide near aperture (n = 117), each producing a small, hyaline drop of conidia. Secondary conidiophores bi- to quaterverticillate, solitary or aggregated but not sporodochial, generally arising from strands of aerial mycelium, particularly around the colony centre; branches and phialides adpressed, primary branches sometimes divergent; stipe of similar length to the height of the penicillus or longer, 60–110 µm long, 3.5–6.5 µm wide at base; penicillus 30–60 µm high, 16–50 µm diam at widest point; phialides straight to slightly curved, slightly flask-shaped, with widest point below the middle, slightly tapering in the upper part, without visible collarette, (5.6–)10.6–12.4–14.4(–19.6) µm long, (1.2–)2.0–2.4–2.6(–3.2) µm wide at base, (1.6–)2.4–2.6–2.8 (–3.6) µm at widest point, (0.8–)1.2–1.4–1.4(–1.8) µm wide near aperture (n = 163); intercalary phialides rare below whorls of terminal phialides, with 3.5–5.5 µm long necks (n = 15). **Conidia** from secondary conidiophores slightly curved, with one slightly flattened side, distally broadly rounded, with laterally displaced hila, (4.2–)4.8–5.2–5.6(–6.6) × (2–)2.4–2.8–3(–3.4) µm (n = 178), held in imbricate, long, white, yellowish white, or orange-white columns that can collapse to form slimy masses over several conidiophores; conidia from primary conidiophores larger, frequently less curved, sometimes without a visible hilum, (5.2–)7.6–8.2–9.0(–15.4) × (2.2–)2.8–3.2–3.4(–4.8) µm (n = 164). **Perithecia** formed frequently in single ascospore isolates, rarely also in conidial isolates (CBS 438.68, CBS 438.70, CBS 222.93), crowded in large numbers on a well-developed stroma, rarely solitary from the mycelium.

Lectotype for *Nectria ochroleuca* (Samuels, 1976a): U.S.A. NORTH CAROLINA: Salem; on bark; Schweinitz 1418 (PH, Collins Set no. 169). **Neotype for *Clonostachys rosea*** (Schroers *et al*., 1999b): NETHERLANDS. Soil; on buried sclerotia of *Sclerotinia minor*; A. van Zaayen & W. Gams (herb. CBS; dried culture ex CBS 710.86, derived from conidia).

Known distribution: Holomorph possibly pantropical, rare in temperate regions; anamorph known from temperate and tropical regions.

Habitat: Perithecia on bark of recently dead trees, frequently occurring often on or near ascomata of subcortical or superficial ascomycetes; conidiophores and/or through bark erumpent sporodochia frequently on bark, frequently associating the perithecia; anamorph frequently isolated from various soil types and decaying plant material (Domsch *et al*., 1980). The species is known as a destructive mycoparasite, coiling around, penetrating, and growing inside fungal host hyphae, used as a biocontrol agent of plant-pathogenic fungi, infrequently isolated from dead insects, and known as a parasite of living nematodes, ticks, and myxomycetes.

Published descriptions and illustrations of the holomorph: Seaver (1909b), Dingley (1951, 1957), Samuels (1976a), Schroers & Samuels (1997), Schroers *et al*. (1999b); of the anamorph: Corda (1839), Bainier (1907b), Thom (1910), Pinkerton (1936), Raper and Thom (1949), Isaac (1954), Udagawa and Horie (1971), Domsch *et al*. (1980).

Additional specimens and ascospore isolates examined: BRAZIL. 1–3 km S of central portion of Serra Araca, 0.8 km E of Rio Jauarí, 00°49’ N, 63°19’ W, 60 m alt.; on vine; Mar 1984; G.J.S. (NY; G.J.S. 626). – Manaus, Reserva Forestal Ducke; on bark; 1 Nov 1977; G.J.S., D. Hosford, W. Buck, E. Ferreira (NY; G.J.S. BR 26; CBS 245.78). – Nova Era; on dead wood; C.S. Hodges (Hodges No. 20; CBS 216.74). – Parà, Belem, Ilha do Combu, Estacão Experimental Combu, 30°60’ N, 48°27’ W, 0 m alt.; on decaying pod of *Theobroma cacao*; Jan 1989; G.J.S., K.F. Rodrigues (NY; G.J.S. 6203; G.J.S. isolate 89-4). – Perimetral Norte Highway, 45 km W of Caracaraí Fazenda Repartimento, Igarapé Repartimento do Ajaraní, 02°01’ N, 61°28’ W; on bark; 31 Jan 1984; G.J.S. (NY; G.J.S. 42; G.J.S. isolate 84-199). – Perimetral Norte Highway, Plateau of Serra Araca, N side of North Mountain, in cloud forest, 00°57’ N, 63°21’ W, 1250 m alt.; on twig; G.J.S., G.T. Prance, J. Pipoly (NY; G.J.S. 481). – CZECH REPUBLIC. Príbram; air in uranium mine; 1967; O. Fassatiová (CBS 438.68). – ECUADOR. Prov. Cotopaxi: *Ca* 100 km from Latmaga, on the Latacunga Quevedo Rd., 1730 m alt.;

on unidentified monocotyledonous stem; 23 Jul 1975; K.P.D., S.E. Carpenter, P. Buriticá (NY; Dumont-EC 1217). – FRANCE. Biados (40); on *Salix* sp.; F. Candoussau and J.-F. Magni; no. A 94147 (BPI 806266; Samuels culture 95-7, CBS 406.95). – 'Le Guillaume' (St Paul), Ile de la Réunion; on *Rhydidhysteron rufulum*; 24 Apr 1997; G. Gilles (BPI. FC 492; CBS 834.97). – Landes, Parc Chateau de Brandos 40, 20 km from Bayonne; on bark; 6 Dec 1992; F. Candoussau (BPI 802563; G.J.S. 93-8). – Îlot de Sauveterre de Béarn, 100 m alt.; on bark of dead ?*Populus nigra*; 25 Oct 1998; G.J.S., F. Candoussau (BPI; CBS 102420). – GUYANA. Vic. Kopinang Village, disturbed forest, 04°58' N, 59°50' W, 670 m alt.; on live rachis of *Pteridium aquilinum*; 24 Jun 1989; G.J.S., B.M. Boom, G. Bacchus (NY; G.J.S. 6232A; G.J.S. isolate 89-29, CBS 193.93). – Ibid.; on bark of recently dead tree (NY, BRG; G.J.S. 6245; G.J.S. isolate 89-37). – JAMAICA. Chester Vale, wet mountainous region, 1000-1300 m alt.; on wood; 21–24 Dec 1908; W.A. Murrill, E.L. Murrill (NY; Murrill 390). – Portland Parish, 1.6 km S of Tranquility, along highway; on *Artocarpus altilis*; 14 Jan 1971; R.P. Korf *et al*. (NY; CUP-MJ 893, A.Y.R. 475; G.J.S. isolate 71-82). – Border between Portland and St. Andrew Parish, traveller's rest, Silver Hill Gap, 25 mile marker from Kingston; on wood; 8 Jan 1971; R.P. Korf *et al*. (NY; CUP-MJ 725; C.T.R. isolate 71-18). – St. Mary Parish, between Buff Bay and Anotto Bay at mile marker 36; on wood; 19 Jan 1971; R.P. Korf *et al*. (NY; CUP-MJ; 965). – St. Thomas Parish, along brittle path from New Castle to Gordontown, below point where trail crosses road to Newcastle; on wood; 20 Jan 1971; R.P. Korf *et al*. (NY; CUP-MJ 948). – St. Thomas Parish, trail between Barrett's Gap and Corn Puss Gap, 530–660 m alt.; on wood; 14 Jan 1971; R.P. Korf *et al*. (NY; CUP-MJ 863). – JAPAN. Shiga Prefecture, Otsu, Omi-jingu, Toshiho Uyeda comm.; on ascocarp of *Hydnotrya tulasnei*; 5 Jul 1975; J.M. Trappe (NY; Trappe 4296). – MEXICO. State of Veracruz, Laguna Verde; on dead leaves of arborescent *Yucca* sp. in cow pasture; 12 Oct 1994; G. Bills (BPI; CBS 916.97, G.J.S. 94-122). – NEW ZEALAND. Auckland: Thames Co., Coromandel Forest Park, Kauaeranga River, Nature Trail to Hoffman's Pool; on *Coprosma* sp.; 15 Aug 1973; G.J.S. (PDD 32680; G.J.S. isolate 73-171, CBS 190.94). – Waitemata Co., Titirangi, Atkinson Park; 5 Sept 1973; on bark of *Hoheria populnea*; J.M. Dingley (PDD 32441; G.J.S. isolate 73-190). – Waitemata Co., Waiatarua, Nature Track; 21 Mar 1973; on bark; J.M. Dingley, G.J.S., C. Samuels (PDD 30636; G.J.S. isolate 73-16, CBS 189.94). – Waitemata Co., Waitakere Ranges, vic. Kitekite Stream, along Marguerite Track; on *Freycinetia* sp.; 30 May 1973; J.M. Dingley, G.J.S., S. Haydon (PDD 31798; G.J.S. isolate 73-93). – Waitemata Co., Wenderholm Scenic Reserve; on bark of *Corynocarpus laevigatus*; 26 Sept 1973; J.M. Dingley, G.J.S., S. Haydon, J.D. Fletcher (PDD 32654; G.J.S. isolate 73-201). – Northland: Hokianga Co., Waipoua Forest, vic. Te Matua Ngahere; on unidentified bark; 31 May 1982; G.J.S., P.R. Johnston, A.P. Hawthorne, R.H. Petersen (PDD 44312; G.J.S. isolate 82-94). – PANAMA. Prov. Panama: Summit of Cerro Jefe, *ca* 23 km N of Pan-American Highway, *ca* 1000 m alt.; on fruit of unidentified palm; 11 Jun 1975; K.P.D., S.E. Carpenter, S.M. Carpenter, S.A. Mori (NY; Pa 63, 76). – SOUTH AFRICA. Eastern Transvaal, Lydenburg; on *Protea cynaroides*; May 1988; M.J. Wingfield (NY; Wingfield 1202). – U.S.A. On decaying bulb of *Lilium auratum*; Jan 1955; E.B. Smalley (CBS 194.57, ATCC 12881, IMI 071095, ex-type strains of *Nectria gliocladioides* Smalley & Hansen). – GEORGIA: Monkey Lake at landing, Suwanne Canal, Recreation Area, Wildlife Refuge, Okefenoka Swamp and vic.; on bark of dead limb; 28 Aug 1978; J.L. Crane, J.D. Schoknecht (NY; C.T.R. isolate 78-227). – NEW JERSEY: Newfield; on *Magnolia*; 20 Dec 1884; G.B. Ellis (NY), Nov 1880, G.B. Ellis 652 (NY), Oct 1881, G.B. Ellis (NY). – NORTH CAROLINA: Macon County, Blue Valley Rd., along E fork of Overflow Creek; on wood; 1 Sept 1994; G.J.S., H.-J. Schroers (G.J.S. isolate 94-39). – Salem; Schweinitz collection ex Collins set (BPI 800415). – OHIO: Hocking Co., Hocking State Park, Crane Hollow; 1 Sept 1968 (C.T.R. isolate 68-120 ss2; CBS 293.78). – PENNSYLVANIA: Chester County, woods W of Experimental Greenhouses, Longwood Gardens, Kennett Square; on dead branches of *Liriodendron tulipifera*; 14 Oct 1978; C.T.R., D.G. Huttleston (NY; C.T.R. isolate 78-206B). – Mercer County, Grove City, old city dump, at the foot of Gilmore St.; on *Acer*; G.J.S.; 14 Oct 1972 (NY; C.T.R. isolate 72-373). – WASHINGTON D.C.: Greenhouse; on *Yucca* sp.; 17 Feb 1903; C.L. Shear, A.J. Watson (BPI 550629). – SOUTH CAROLINA: Oconee County, Sumter National Forest, 2 miles south of junction of Whitewater–Salem Road; on trunk of ?*Liriodendron*; 5 Oct 1972; C.T.R. & G.J.S. (NY; C.T.R. 72-344). – KANSAS: Pottawatomie County, woods 5 miles E of Manhatten; on dead twigs; 22 Oct 1951; C.T. R., R.L. Shaffer (NY; C.T.R. 3609). – WISCONSIN: Ravine, Kalama; on bark of *Acer circinatum*; 10 Dec 1909; Humphrey 6197 (NY). – VENEZUELA. Edo. Trujillo: Road between Escuque and La Mesa de San Pedro; on wood of *Cecropia* sp.; 31 Jul 1971; K.P.D., G.J.S. (NY; Dumont-VE 3477). – Parque Nacional Guaramacal, *ca* 10 km SW of Batatal, La Defensa, along Río Saguás, Campamiento Granja Bocono, in disturbed vegetation along river, 09°19'N, 70°09'W, 2000 m alt.; on bark; 20 Nov 1990; G.J.S., B. Hein, S. M. Huhndorf 7356 (BPI, NY, VEN; G.J.S. isolate 90-167, CBS 193.94). – Edo. Sucre: along the road between Mundo Nuevo and Manacal, *ca* 6-10 km N of Route 9, NW of Irapa; on unidentified bark; 7 Jul 1972; K.P.D., R.F. Cain, G.J.S., G. Morillo, J. Farfan (NY; Dumont-VE 4136; C.T.R. isolate 72-114). – *Ca* 30 min walk along trail N of Manacal, NW of Irapa; on unidentified bark; 9 Jul 1972; K.P.D., R.F. Cain, G.J.S., G. Morillo, J. Farfan (NY; Dumont-VE 4551; C.T.R. isolate 72-93). – *Ca* 9 km N of El Rincon on Carupano–El Pilar Road; on unidentified bark; 6 Jul 1972; K.P.D., R.F. Cain, G.J.S., G. Morillo (NY; Dumont-VE 4073; C.T.R. isolate 72-81). – Edo. Tachira: Along the road Zumbador–Quieniguea; on unidentified wood; 29 Jul 1971; K.P.D., G.J.S., L. Borjas (NY, VEN; Dumont-VE 3373). – Edo. Yaracuy: In mountains N of Nirgua; on unidentified wood; 7 Jul 1971; K.P.D. *et al*. (NY; Dumont-VE 1577; C.T.R. isolate 71-239). – Ibid. (NY; Dumont-VE 1612; C.T.R. isolate 71-291). – Edo. Monsagas: La Carmelita, Hacienda Las Acacias, vic. Caripe; on unidentified wood; 17 Jul 1972; K.P.D., R.F. Cain, G.J.S., G. Morillo, F. Malave (NY, VEN; Dumont-VE 5252). – Vic. of 'Cueva del Guácharo', Caripe; on unidentified vine; 18 Jul 1972; K.P.D. *et al*. (NY; Dumont-VE 5320; C.T.R. isolate 72-146). – On petiole of *Cecropia* sp. (NY; Dumont-VE 5233; C.T.R. isolate 72-129). – Edo. Sucre: Trail between Manacal and Los Pocitos, NW of Irapa; on unidentified bark; 10 Jul 1972; K.P.D., R.F. Cain, G.J.S., G. Morillo, J. Farfan (NY, VEN; Dumont-VE 4628; C.T.R. isolate 72-130). – Ibid. (NY; Dumont-VE 4607; C.T.R. isolate 72-103 ss3, CBS 548.79). – Ibid. (NY, VEN; Dumont-VE 4607; C.T.R. isolate 72-103). – Edo. Miranda: Parque Nac. El Avila, vic. Quebrada Los Palos Grandes, south-facing slope of La Silla; on unidentified bark; 2 Jul 1972; K.P.D., G.J.S., B. Manara (NY; Dumont-VE 3638).

Additional conidial isolates or anamorphic specimens examined: ARMENIA. From soil (CBS 907.72D, VKM F-1675*). – From stone covered with moss (CBS 907.72E, VKM F-1676*). – AUSTRALIA. From wheat; 1998; S.-L. Leong (CBS 100494, FRR 5189). – AZERBAIJAN. From soil under tree (CBS 907.72G, VKM F-1678*). – CZECH REPUBLIC. On fruit of *Aesculus hippocastanus* (PRM; type of *Tubercularia carpogena*; no conidiophores visible). – On forest soil [iconotype of *Clonostachys araucaria*; no type preserved at PRM; conidiophores illustrated by Corda (1839: Pl. XV, 2, 3) are similar to the

secondary conidiophores found in species of subgen. *Bionectria* in their penicillate appearance, penicillus–stipe proportions, and imbricate conidial columns; the conidia were described as ovoidal to ellipsoidal, without a visible hilum]. – FRANCE. From rotten cardboard; G. Bainier (CBS 100502, NRRL 1084, DAOM 215946, Thom No. 454-4640.428; ?ex-type strain of *Gliocladium roseum* Bain.; received by Thom from da Fonseca; strains sent by da Fonseca are considered to be those studied by Bainier; Pinkerton (1936) remarked that the strain Thom '454-4640.428' came 'from Král in Prague, Bohemia'). – Saucisse; on tuber of *Solanum tuberosum* (ex-type strain of *V. foexii*, CBS 117.23). – GERMANY. Hoyerswerda; on dead branches of *Rosa* sp. [slide W.G. 2639 (herb. CBS), ex type of *Torula rosea* (B), containing secondary conidiophores and sporodochia]. – NETHERLANDS. On *Wistaria sinensis*; A. Jaarsveld (CBS 188.33). – Isolated from biofilter for the purification of styrene-containing gases; H.H.J. Cox, TNO-Milieu en Energie, Delft, No. A24 (CBS 102.94, isolated from a sector forming white conidial masses of a colony that formed green conidial masses otherwise (filed as 103.94). – SLOVENIA. Cave near Mengore, near Tolmin; cadaver of *Troglophilus neglectus* in cave; 1 Feb 1996; S. Jeram, P. Zalar (CBS 997.97, MZKI-B-511). – TUNISIA. From xylem of diseased apricot tree; 1975; B. Jamoussi (CBS 649.80). – UKRAINE. From soil in conifer-*Betula* forest (CBS 907.72J, VKM F-1682*). – Crimea, Ay-Petry Mountain; forest soil (CBS 907.72C, VKM F-1674*). – Crimea, Yalta, Nikitskij Botanic Garden; soil (CBS 907.72A, VKM F-1672*). – Ibid. (CBS 907.72B, VKM F-1673*). – Kharkov; fruit of *Quercus* sp.; L.A. Belyakova (CBS 224.72F, VKM F-153). – Zakarpat Region; soil; in young *Fagus* forest; A.A. Milko (CBS 148.72, VKM F-1645). – U.K. E.M. Wakefield (CBS 178.28, MUCL 7998). – Corsham, Wilts; on decayed *Elaphomyces* [K; Berk. & Br. 533, slide W.G. 2698 (herb. CBS), ex type of *Verticillium epimyces*, containing sporodochia and conidial columns. The original illustration shows a penicillate conidiophore representative of *C. rosea* (Berkeley & Broome, 1851, Pl. VII, 15); the conidial size is recorded with a length 4–5 times longer than their width and thus would differ from *C. rosea*]. – U.S.A. On decaying gourds (Berkeley no. 672, slide W.G. 2880 (herb. CBS) ex PC, ex type of *Verticillium stigmatellum*, containing solitary secondary conidiophores with conidial columns; the original description states: '*floccis in glomerulas minimas collectis sursum ramosis verticillatis*; *sporis parvis ellipticis*', thus matching the characters of secondary conidiophores of *C. rosea*). – MASSACHUSETTS: East Hampton; on *Acer palmatum*; 1950; M.A. McKenzie (ex-type strain of *Verticillium intertextum* Isaac & Davies; CBS 376.55, IMI 061295). – NEW JERSEY: Isolated from soil of eggplant field; A.P. Keinath, Keinath 331, NS 35 (CBS 704.97). – Newfield; on bark of *Magnolia*; 1882 [slide W.G. 3432 (herb. CBS) ex Ellis 3582 (Herb. Chicago 585), containing secondary conidiophores and sporodochia with conidia typical of *C. rosea*; previously identified as *Dendrodochium rubellum* Sacc. var. *macrosporum* Sacc.]. – NEW YORK: Causing lesions on stored carrot roots; W.E. Rader (CBS 226.48, ATCC 10406, MUCL 7996; ex-type strain of *Gliocladium aureum*). – Isolated from soil; J.P. Stack, No. NS 31 (CBS 708.97). – MARYLAND: Isolated from forest soil; A.P. Keinath No. 931, NS 33 (CBS 706.97). – Isolated from wheat straw; No. NS 30 (CBS 709.97). – Beltsville; isolated from *Ixodes* sp.; 1997; P.C. Allen (G.J.S. isolate 97-10, CBS 912.97). – OHIO: Hocking Co., Hocking State Park, Crane Hollow; from *Hypomyces armeniacus* on ground; 1 Sept 1968; C.T.R. (CBS 287.78, C.T.R. isolate 68-109). – WASHINGTON. From soil; K.B. Raper (CBS 229.48, ATCC 10521, DSM 1165, IMI 040024, NRRL 1085).

Asterisks indicate VKM-strains received as *Gliocladium verticillioides* Pidoplichko.

Clonostachys rosea f. **catenulata** (Gilman & Abbott) Schroers, *stat. nov.* — Fig. 16 a–c.

≡ *Gliocladium catenulatum* Gilman & Abbott, Iowa St. Coll. J. Sci. 1: 303. 1927.

= *Gliocladium varians* Pidoplichko, Khran. sakharn. Svekly 1: 369. 1930; Fungus flora of coarse fodders: 198. 1931 [synonymy according to Domsch *et al*. (1980)].

= *Gliocladium roseum* var. *viride* Rall, Mycologia 57: 877. 1965 (as *G. roseum* (Link) Bainier var. *viride*).

Description from culture only of conidial isolates: Colonies reaching 40–50 mm diam in 7 d at 24ºC; optimum for growth 27°C (45–55 mm diam); maximum 33/36°C. Colony reverse on OA greyish green to olivaceous-green or pale to light yellow or pale orange (2A4–4A24–5A4) after incubation in darkness and under day-light, generally light orange (5–6A4) when incubated under UV, in older colonies generally with greenish hues because of the colour of conidial masses, frequently with yellow pigments at the margin and outside the colony. Colony surface on OA and CMD granular because of conidial masses or felty to cottony because of strands of the aerial mycelium; surface unpigmented or greenish grey to olivaceous because of conidial masses, on OA with strong production of aerial mycelium but sparse sporulation. **Conidiophores** as in *C. rosea* f. *rosea*. Phialides in whorls of 2–5, (25–) 29–31–37(–45) µm long, (1.6–)2–2.2–2.4(–3) µm wide at base, (1–)1.4–1.6–1.6(–2) µm wide near aperture (n = 87), each producing a small, hyaline drop of conidia. Secondary conidiophores: phialides (8–)10.4–12–14(–18) µm long, (2–)2.2–2.2–2.4(–2.8) µm wide at base, 2.4–3.0 µm at widest point, 1–1.8 µm wide near aperture (n = 33). **Conidial masses** of similar shape as in *C. rosea* f. *rosea*, uncoloured or greenish hyaline on the primary conidiophores, white, with time turning green, to olivaceous-green on the secondary conidiophores. **Conidia** hyaline, minutely curved, distally broadly rounded or slightly tapering, with a laterally displaced hilum, those from secondary conidiophores (4–)4.8–5–5.4(–6) × (2.2–)2.4–2.6–2.8(–3) µm (n = 71), those from primary conidiophores slightly longer, 5.6–10 × 2–3.6 µm. Sporodochia not observed. Perithecia and stroma not observed.

Known distribution: Known from northern temperate regions and Australia.

Habitat: Mainly isolated from soil; known as a destructive mycoparasites, used as biocontrol agents of plant-pathogenic fungi.

Type for *Gliocladium catenulatum*: U.S.A. UTAH: From soil; 1927; E.V. Abbott (ex-type strain: CBS 154.27, MUCL 7575).

Published descriptions and illustrations: Domsch *et al*. (1980).

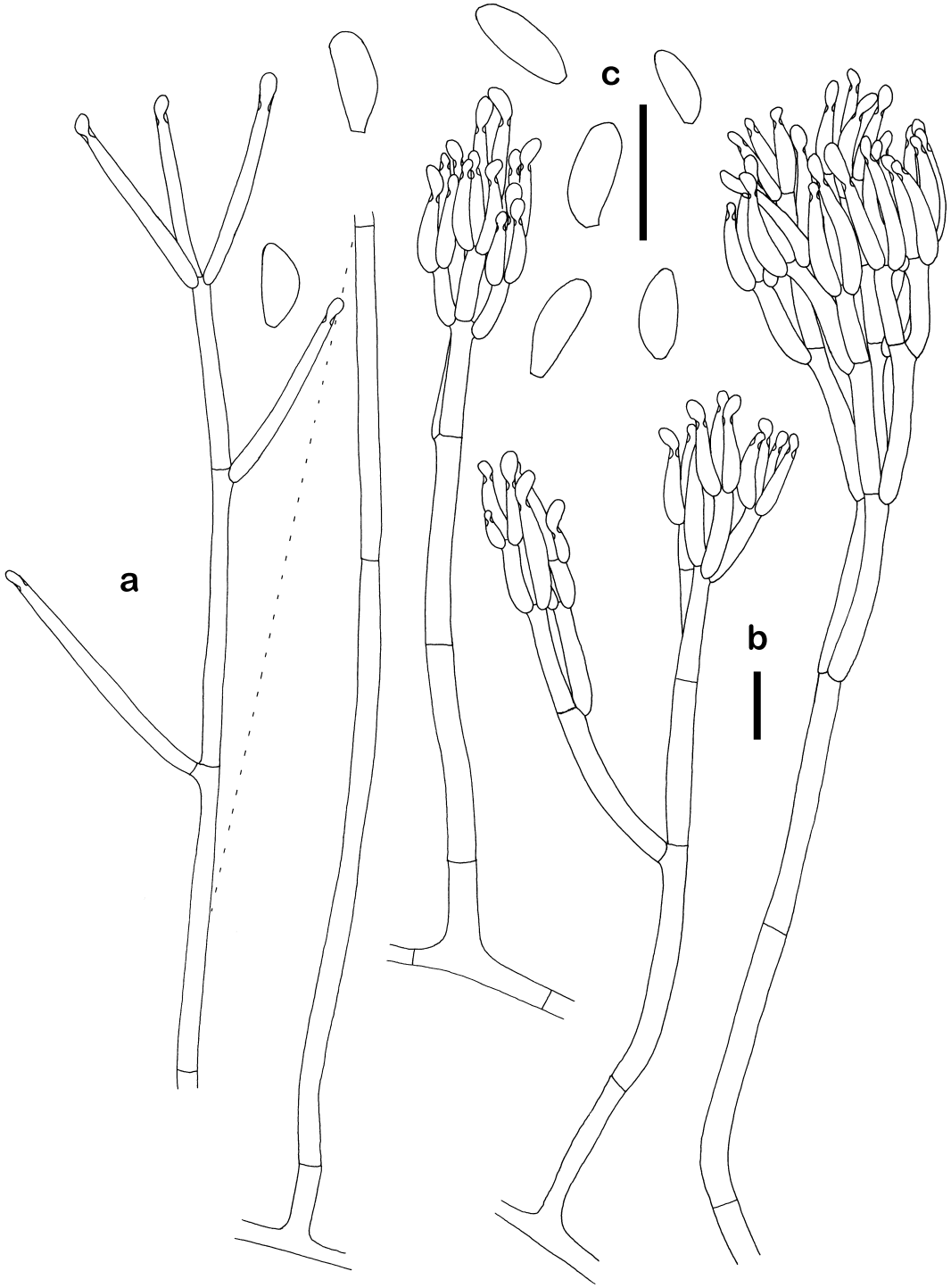


Fig. 16. ***Clonostachys rosea*** f. ***catenulata*****. a.** Primary verticillium-like conidiophore. **b.** Adpressed, secondary conidiophores. **c.** Conidia with laterally displaced hilum. – All from CBS 443.65, 7–10-d-old OA cultures. Scale bars = 10 µm; the shorter bar applies to a, b, the longer to c.

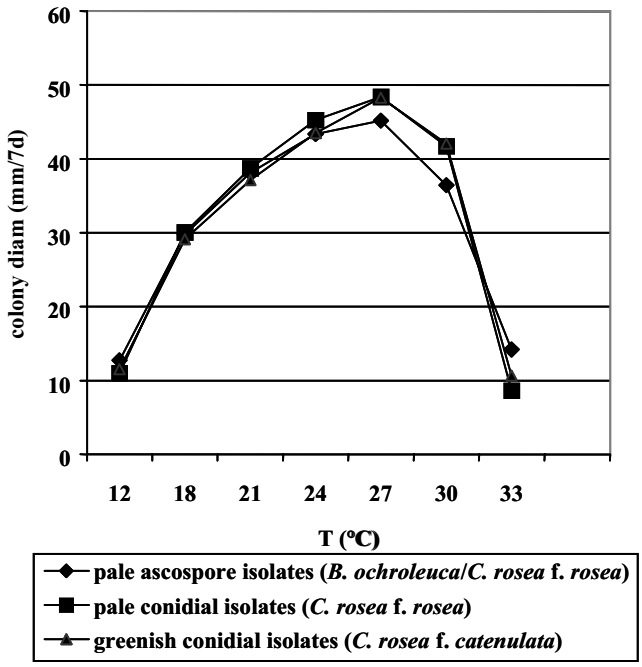


Fig. 17. Colony diameters of each taxon are averages based on studies of several strains.

Additional strains examined: AUSTRALIA. From wheat; 1998; S.-L. Leong (CBS 100495, FRR 5190 ?). – GERMANY. Kiel-Kitzeberg; wheat-field soil; W. Gams (CBS 221.72b). – NETHERLANDS. From biofilter for the purification of styrene-containing gases; H.H.J. Cox (TNO-Milieu en Energie, Delft) No. A24 (CBS 103.94, isolated from a colony that also formed a sector with white conidial masses filed as 102.94). – SWITZERLAND. Hoffmann-La Roche (CBS 569.69). – UKRAINE. From peat (CBS 125.72, VKM F-853). – From soil; Kirilenko (CBS 126.72, VKM F-1095). – U.S.A. MASSACHUSETTS: East Hampton; on *Acer palmatum*; 1950; M.A. McKenzie (ex-type strain of *Verticillium intertextum* Isaac & Davies; CBS 376.55, IMI 061295). – WYOMING: Medicine Bow Mountains, Libby Flats; from soil; Oct 1961; G. Rall, No. R. 67 (CBS 443.65, ATCC 16389, ex-type strain of *Gliocladium roseum* var. *viride*). – USSR: CBS 511.66 (VKM F-790); all three cultures from VKM were received as *Gliocladium varians.*

Notes: The teleomorph of *Bionectria ochroleuca* is frequently encountered in tropical and, less commonly, in temperate regions. Because of its smooth to slightly rough perithecia, *B. ochroleuca* is distinct from species with coarser perithecial warts like *B. apocyni*, *B. oblongispora*, *B. byssicola*, and *B. capitata*. As in these species, cells with unevenly thickened walls are commonly found in their outermost layers (Fig. 10, Schroers *et al*., 1999b). Such cells were rarely encountered in other species of subgenus *Bionectria* with entirely smooth perithecia, such as *B. compactiuscula*, *B. solani*, *B. aureofulvella*, *B. pseudochroleuca*, and *B. pseudostriata*. Because of overlapping size ranges of ascospores, *B. ochroleuca* is hardly distinct from other species with smooth perithecia based only on the teleomorph.

Anamorphs obtained from ascospores of *B. ochroleuca* are morphologically indistinguishable from conidial isolates of *C. rosea*. The link of both morphs was first established by Dingley (1951, as *Verticillium tubercularioides* Speg.) and Smalley & Hansen (1957), and subsequently accepted by numerous authors, for example Samuels (1976a), Domsch *et al*. (1980), and Schroers *et al*. (1999b). Only strains with white to pale orange conidial colours, characterized as *C. rosea* f. *rosea*, have been linked to a *Bionectria* teleomorph.

Strains of *C. rosea* f. *catenulata* (formerly *G. catenulatum*) have not been linked to a teleomorph, but are morphologically indistinguishable from *B. ochroleuca*/*C. rosea* apart from the green colour of the conidial masses. The interpretation of *Gliocladium catenulatum* as a form of *C. rosea* is suggested by several arguments. (1) The varieties have identical conidiophore branching patterns and conidia. The primary conidiophores are verticillium-like, sparsely branched, and generally form side branches only in the upper part, rarely from lower parts of the stipe (Figs 16 a; 36 f). The secondary conidiophores are adpressed or rarely show somewhat divergent primary branches that result in independent penicillate units (Fig. 16 b, middle; Figs 25–28, 32, 33 in Schroers *et al*., 1999b). (2) The varieties have identical growth rates at various temperatures (Fig. 17); (3) the green pigmentation of the conidial masses and colony reverse is variable among the strains referred to this taxon. Several strains of *C. rosea* f. *catenulata* form the green pigment only in old colonies. Many strains tend to form sectors in colonies where white or green conidial masses alternate even when freshly isolated. Subcultures from white sectors in otherwise green colonies (e.g. CBS 102.94 isolated from a sector of CBS 103.94 and those of CBS 154.27, ex-type strain of *G. catenulatum*) remain white and would be identified as *C. rosea* f. *rosea*. Among all morphological characters, the two varieties differ only in conidial pigmentation; (4) strains of both varieties also exhibit the same kind of destructive mycoparasitism and both are used in the biocontrol of fungal plant pathogens. (5) Sequences of *tub*2, ITS-1, and ITS-2 for conidial isolates of both varieties (from different origin in the temperate regions) are almost identical, with the exception of the ex-type strain of *G. roseum* var. *viride* that exhibits 9 apomorphic nucleotide changes and a gap of three nucleotides in the *tub*2 when compared with other conidial isolates of *C. rosea* (Figs 4 a–c).

The name of the new form could equally be taken either from that of a species or a variety. The preference is given to the older and better-known epithet *catenulatum*.

The close relatedness of conidial isolates and ascospore isolates is supported by bootstrap analyses (bootstrap values: 97 in Fig. 2; 90 in Fig. 3; 90 in Fig. 4 a: P; 96 in Fig. 4 b: P; 91 in Fig. 5). This supported clade is considered the species clade of *B. ochroleuca*/*C.*

rosea including strains with white to pale orange as well as green conidial masses. The conidial isolates of *C. rosea* f. *rosea* and f. *catenulata*, however, are not identical to ascospore isolates. Based particularly on nucleotide differences of the *tub*2-introns two clades are evident comprising either conidial or ascospore isolates (Figs 3, 4 a–c). The clade comprising the ascospore isolates always received bootstrap support (Figs 3, 4), while that comprising the conidial isolates is supported only in the analyses of Fig. 3. The segregation of both clades indicates that the conidial isolates have their own phylogenetic history. They may represent clonal lineages derived from sexually reproductive strains. In one conidial isolate, CBS 438.68, which appears more closely related to other conidial isolates (Fig. 4 b, c), however, perithecia are formed in culture. In contrast, perithecia were not found in other conidial isolates, while they were frequently formed in ascospore isolates. The close relatedness of strains of *C. rosea* f. *rosea* and f. *catenulata*, on the other hand, indicates that they may have the same phylogenetic history, which is also supported by phenotypical evidence (see above).

The size and shape of conidial columns are correlated to some extent with the branching patterns of the secondary conidiophores. *Bionectria ochroleuca* normally forms narrow and rather long conidial columns because of its adpressed branches and phialides. Species with more divergent branches and phialides in the secondary conidiophores form rather short and broad columns. *Bionectria compactiuscula* is intermediate, having several long and narrow columns on the penicillus of the same conidiophore as a result of divergent primary branches that terminate in several independent narrow penicilli (Fig. 32 a).

Secondary conidiophores of *C. rosea* and *B. pseudochroleuca* (Fig. 43 d) are indistinguishable. The species differ in the morphology of the primary conidiophores. In *B. pseudochroleuca*, the phialides of the primary conidiophores are adpressed (as they are in species of the *C. solani* complex) but formed on somewhat divergent metulae. Because of the divergence of the metulae and because only a few phialides are formed on metulae in *B. pseudochroleuca*, however, the primary conidiophores can appear similar to the verticillium-like habit seen in *C. rosea* when colonies are observed by the dissecting microscope. Primary conidiophores of *B. byssicola* differ from those of *B. ochroleuca* in the more frequent occurrence of long lateral branches arising from near the base of the conidiophores (Fig. 19 c). Such lateral branches are rare in *B. ochroleuca* / *C. rosea*.

The primary conidiophores of *B. ochroleuca* are formed earlier than the secondary ones and predominate towards the colony margin. The secondary conidiophores frequently arise from hyphal strands in older parts of the colony. The type strain of *Verticillium intertextum* (CBS 376.55) differs from other isolates of the species in lacking secondary conidiophores and generally lacking aerial mycelium, particularly hyphal strands. The conspecifity of *V. intertextum* and typical strains of *C. rosea*, however, is indicated by molecular data (Fig. 4 a–c). Consequently, *V. intertexum* is here interpreted as a synonym of *C. rosea*. The ex-type strain of *V. intertextum* intergrades morphologically with *C. rhizophaga*, which is characterized by the very poor production of secondary conidiophores and abundant verticillium-like primary conidiophores. Recognition of the latter species is mainly based on molecular data.

The ex-type strain of *Nectria gliocladioides* differs from the anamorph of other strains in the sparse formation of aerial mycelium and more sparsely and irregularly branched secondary conidiophores (Smalley and Hansen, 1957: Fig. 5). Smalley and Hansen (1957) interpreted these as intermediates between the verticillium-like (their Fig. 1) and the penicillate conidiophores (their Fig. 2). The asci and ascospores as described by Smalley and Hansen (1957) fall within the range of those of *B. ochroleuca*. Based on the *tub*2 sequences (Fig. 4 a–c), *Nectria gliocladioides* clusters among strains of *B. ochroleuca*, supporting the synonymy.

The recognition of *B. aureofulva* as a synonym of *B. ochroleuca* is based on perithecial wall anatomy (compare the present Fig. 35 d, k with Fig. 9 in Schroers *et al*. (1999b), habit of the perithecia, and geographical occurrence of the type specimens (eastern U.S.A.). *Bionectria aureofulva* was incorrectly accepted as the name for the species that is here recognized as *B. samuelsii* [Samuels (1976a); Samuels *et al*., 1990; Schroers & Samuels (1997); Rossman *et al*., 1999; Rossman *et al*. (2001)].

6. Bionectria byssicola (Berk. & Broome) Schroers & Samuels, Z. Mykol. 63: 152. 1997. — Figs 18 a–k, 19 a–b.

≡ *Nectria byssicola* Berk. & Broome, J. Linn. Soc., Bot. 14: 116. 1873.
≡ *Cucurbitaria byssicola* (Berk. & Broome) O. Kuntze, Rev. Gen. Plant. 3: 460. 1898.
= *Nectria manihotis* Rick, *in* Theissen, Ann. Mycol. 8: 458. 1897.
= *Nectriella farinosa* Hennings, Hedwigia 36: 219. 1897.
≡ *Nectria farinosa* (Hennings) A. Möller, Phycomyceten und Ascomyceten, *in* A.F.W. Schimper, Bot. Mitt. Tropen 9: 296. 1901.
= *Nectria prorumpens* Rehm, Hedwigia 39: 221. 1990.

Anamorph: ***Clonostachys byssicola*** Schroers, *stat. nov*. — Fig. 19 c–f.

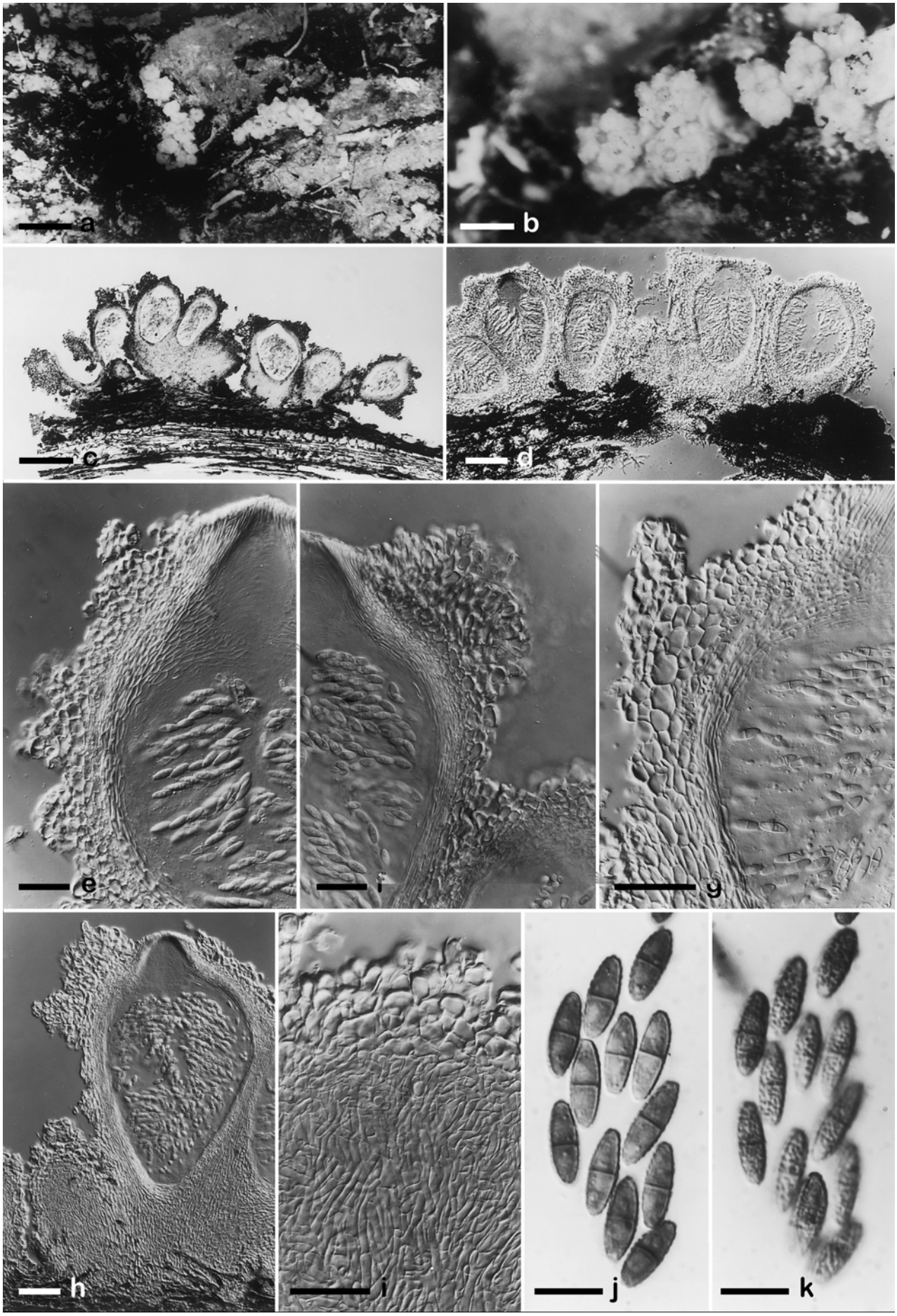
Clonostachydi roseae similis sed conidiophoris primariis saepe prope basim ramosis; conidiophoris secundariis in pustulis vel sporodochiis in superficie agari vel mycelio aerio fasciculato dense aggregatis; rami seu acute divergentes seu sporodochialia compressa. Conidia *Clonostachydi roseae* similia, (3.2–)4.4–5.2–5.8(–10.8) × (1.8–)2.4–2.6–2.8(–4) µm, illa conidiophororum secundariorum saepe breviora quam 5 µm, 3.2–4.8 × 2.8–3.8 µm.

Holotypus anamorphosis: NY; cultura sicca, isolata ex specimine Dumont-VE 4681 (NY); isotypus herb. CBS; cultura viva CBS 364.78.

Description from natural substratum: Stroma superficial to erumpent through bark, bearing sporodochia or perithecia; cells angular to subglobose. **Perithecia** sometimes solitary, mostly crowded of 10 to 50, subglobose to oval, (150)–250–400 µm high, 100–315 µm diam, laterally pinched when dry, warted to rough, orange to brownish orange, particularly the ostiolar region, minutely papillate or not papillate. **Perithecial warts** off-white or pale yellowish, to 60 µm high, to 140 µm diam, largest in the upper part of the perithecium or around the ostiole; cells angular to globose, 6.5–10.5 × 5–8.5 µm; outermost cells (5.5–)10–13 (–20) × (3–)6.5–9(–15) µm, with unevenly thickened walls up to 9 µm thick. **Perithecial wall** 30–45 µm thick, composed of three regions. Outer region 10–25 µm or to 4 cells thick; cells angular to globose, (4–)8–9.5–11(–16.5) × (3–)6–7–8(–12) µm, with uniformly thickened walls around 1.5 µm thick; vacuoles frequently observed. Middle region 4–12 µm thick, consisting of up to 4 layers of intertwined hyphae. Inner region 8–17 µm thick. **Asci** narrowly clavate to clavate, (44–)55–60–65(–90) × (5.5–)7.5–8.5–9(–12.5) µm (n = 205), 8-spored; apex rounded, ring visible. **Ascospores** ellipsoidal to oblong-ellipsoidal, spinulose to small-warted, (8.4–)11.2–12.4–13.4(–19.8) × (2.6–)3.8–4.2–4.6(–7.4) µm (n = 821). **Sterile mycelium** generally not formed on the substratum. **Sporodochia** frequently associated with perithecial clusters, robust; conidiophores and hyphae of the subhymenium forming a dense parallel *textura porrecta*.

Description from culture: Colonies reaching 50 mm in 7 d at 24ºC; optimum for growth 24–27°C, maximum 33–>36°C. Colony reverse on OA and PDA pale yellow (4A3) after incubation in darkness and under day-light, to light orange (5–6A5) when incubated under UV. Colony surface finely to coarsely granular because of sporodochia and confluent conidial masses or exudates, or felty to cottony because of strands of the aerial mycelium; surface unpigmented or pale yellowish to pale orange because of the conidial masses. **Conidiophores** dimorphic. Primary conidiophores verticillium-like, formed throughout the colony, dominating towards the margin, arising from the agar surface; main stipe frequently short because of independent side branches arising from near the base, 10–100 µm long, 3–5 µm wide at base; branched part 20–100 µm high; phialides in whorls of 2–4, divergent or divergent at acute angles, sometimes singly, particularly when arising from lower levels, straight, cylindrical, slightly tapering towards the tip, (12.4–)22.6–26.2–29.2(–48) µm long, (1.4–)1.8–2–2.2(–2.8) µm wide at base, (1–)1.4–1.4–1.6(–2) µm wide near aperture (n = 178), each producing a small, hyaline drop of conidia that frequently collapses to form a single head on several phialides of the same metula or of several side-branches; collarette lacking or minute. Secondary conidiophores bi- to quinquiesverticillate, densely aggregated, formed in pustules or sporodochia on the agar surface or from strands of aerial mycelium; branches either divergent at acute angles, or in sporodochia, adpressed; stipes variable, long and frequently intergrading with the subhymenial tissue of sporodochial aggregates, or short when arising laterally from the hyphal strands; phialides in loose whorls of 3–5, straight to slightly curved, narrowly flask-shaped, generally with widest point in the lower third, or almost cylindrical, tapering in the upper part, without a visible collarette, (7.6–)10.8–13.8–15.4(–27.8) µm long, (1.4–)1.8–2–2.2 (–2.8) µm wide at base, (1.4–)2.0–2.4–2.4(–3) µm at widest point, (0.8–)1.2–1.4–1.6(–2) µm wide near aperture (n = 197); intercalary phialides not observed. **Conidial masses** white, pale yellow, or pale orange, normally as watery to slimy dome-shaped masses, less frequently

Fig. 18. ***Bionectria byssicola*. a, b.** Habit of crowded perithecia. **c–h.** Sections through perithecia and ± superficial stroma (c, d, h), lateral perithecial walls and perithecial warts (e–g). **i.** Subsurface view of perithecial wall; walls of unevenly thickened outermost cells; hyphal cells of middle region. **j, k.** Discharged ascospores stained with cotton blue, in optical section (j) and surface view (k), showing small warts. – a, b: G.J.S. 3890; c, f, h, i: Dumont-VE 4681; d, g: G.J.S; e, j, k: U0041. All from natural substratum. a, b: DM; c: LM; others: DIC. Scale bars: a = 750 µm; b = 200 µm; c = 250 µm; d = 100 µm; e–g, i = 30 µm; h = 50 µm; j, k = 10 µm.


a
b
c
d
e
i
g
h
i
j
k

in imbricate chains. **Conidia** hyaline, minutely curved, distally broadly rounded, with a laterally displaced hilum, (3.2–)4.4–5.2–5.8(–10.8) × (1.8–)2.4–2.6–2.8 (–4) µm (n = 903); conidia frequently shorter than 5 µm, particularly those from sporodochia (3.2–4.8 × 2.8–3.8 µm), ovoidal to subglobose but hilum laterally displaced; conidia from primary conidiophores slightly curved to almost ellipsoidal, symmetrically extruded from the phialidic aperture. **Perithecia** not observed. **Sporodochial** subhymenium arranged in a *textura porrecta*.

Type for *Nectria byssicola*: Sri Lanka (Ceylon), locality unknown, Thwaites 173d (K, isotype NY); lectotype: slide 'Ceylon 173 GHKT' (NY), possibly from Thwaites 173a (NY) (designated by Schroers & Samuels, 1997). **Epitype** (designated by Schroers & Samuels, 1997): VENEZUELA. Edo. Sucre: trail from Los Pocitos, 0.5 h walking toward Santa Isabel, NW Irapa; on unidentified wood; 11 Jul 1972; K.P.D., R.F. Cain, G.J.S., G. Morillo, F. Farfan (VEN, NY; Dumont-VE 4681; C.T.R. isolate 72-123, CBS 364.78, ex ascospores). **Type for *Clonostachys byssicola*:** dried culture ex CBS 364.78, filed together with epitype of *B. byssicola* (NY); isotype: herb. CBS.

Known distribution: Tropical to temperate.

Habitat: On bark of recently dead trees; anamorph once reported from stem of living *Persea americana* (*Lauraceae*) with stem dieback symptoms (Dr C.F. Hill, pers. comm.).

Published descriptions and illustrations: Samuels (1976a), Samuels *et al*. (1990), Schroers & Samuels (1997).

Additional specimens/strains examined: BRAZIL. São Paulo: On wood (C.T.R. isolate 66-225, CBS 288.78). – Amazonas: Base of west-facing talus slope of Serra Acraca, near central portion of the Serra about 45 min walk from lower airstrip, tall moist Igapó forest with palm, 00°49' N, 63°19' W, 60 m alt.; on vine; 4 Mar 1984; G.J.S. (NY; G.J.S. 917; G.J.S. isolate 84-271). – FRANCE. Le mez de Boeuf, 2040 m alt.; on *Acacia heterophylla*; 3 May 1985; G. Gilles R 15 (NY). – FRENCH GUIANA. Montagne de Kaw, route de l'est, km 27, 04°60' N, 52°40' W); on hanging fruit of dead *Vochysia* sp.; 21 Mar 1986; G.J.S., C. Feuillet (CAY, NY; G.J.S. 4386; G.J.S. isolate 86-322). – Piste de Saint-Elie, on road between Sinnamary and St. Elie, km 16, 'ECEREX', ORSTOM, research area, 05°20' N, 53° W; on *Hypoxylon* sp.; Feb, Mar 1986; G.J.S. (NY; G.J.S. 3937; CBS 206.93, G.J.S. isolate 86-242). – Ibid.; on decaying petiole of *Cecropia* sp.; Feb, Mar 1986; G.J.S. (NY; G.J.S. 3963; CBS 194.94, G.J.S. isolate 86-244. – NY; G.J.S. 3921; G.J.S. isolate 86-236). – Ibid.; on twigs of recently dead tree; Feb, Mar 1986; G.J.S. (NY; G.J.S. 3890; G.J.S. isolate 86-230). – Saül, *ca* 20 km SW of Saül (03°60' N, 53°20' W), toward Mt. Galbao (03°50' N, 53°20' W), 700–750 m alt.; on deaying petiole of *Cecropia* sp.; 24–28 Jan 1986; G.J.S., J.R. Boise (NY; G.J.S. 3349; CBS 208.93; G.J.S. isolate 86-131). – Upper Marouini River, 2 km N of Oumanfou-Langa Soula, 02°53' N, 54°00' W, 150 m alt.; on dead vine; 23, 24 Aug 1987; G.J.S., J.-J. deGranville, L. Allorge, W. Hahn, M. Hoff, A. Weitzman (CAY, NY: G.J.S. 5980; G.J.S. isolate 87-152, dead). – GUYANA. Cuyuni-Mazaruni Region VII, Mazaruni Subregion VII-2: vic. Chinoweing village, 05°32' N, 60°07' W, 650–750 m alt.; on bark of recently dead tree; 20–23 Feb 1987; G.J.S., J. Pipoly, G. Gharbarran, J. Chin (BPI, NY; G.J.S. 4652). – Along Koatse River, *ca* 2 km E of Pong River, *ca* 5 h walk W of Chinoweing village, 05°28' N, 60°04' W, 600–650 m alt.; on small, dead branches; Feb–Mar 1987; G.J.S., J. Pipoly, G. Gharbarran, J. Chin, R. Edwards (BPI, NY; G.J.S. 4917). – INDONESIA. North Sulawesi, Eastern Dumoga-Bone Natl. Park, vic. Camp Edwards, 00°35' N, 123°51'E, 664 m alt.; on twig; 6, 8 Oct 1985; G.J.S. (BO, NY G.J.S. 2127; CBS 202.93, G.J.S. isolate 85-148). – JAMAICA. St. Thomas Parish, between Wheelerfield and Johnson Mt., *ca* 150 m alt.; on wood; 15 Jan 1971; R.P. Korf *et al*. (NY; CUP-MJ 872; C.T.R. isolate 71-69). – On wood; 15 Jan 1971; R.P. Korf *et al*. (NY; CUP-MJ 878, A.Y.R. 459; C.T.R. isolate 71-71). – Along sulphur river, above Bath Fountain Hotel, *ca* 150 m alt., on wood; 13 Jan 1971; R.P. Korf *et al*. (NY; CUP- MJ 846, A.Y.R. 437; CBS 326.78, C.T.R. isolate 71-59. – NY; CUP-MJ 842, A.Y.R. 432; C.T.R. isolate 71-67). – Border between St. Thomas Parish and Portland Parish, trail from Whitfield Hall to Portland Gap, to Blue Mt.; on wood; 17 Jan 1971; R.P. Korf *et al*. (NY; CUP-MJ 883, A.Y.R. 462; C.T.R. isolate 71-74). – JAPAN. Mt. Mitsumine, Chichibu, Tokyo; Y. Doi; 24 Sept 1967 (NY; D-410). – UGANDA: Swamp Camp, Ruhija Station Bwindi, impenetrable National Park; on *Alchorea* branches; 4 Jul 1995; K.T. Hodge U0041 (BPI; CBS 914.97, G.J.S. isolate 95-131). – NEW ZEALAND. South Auckland, Pukehohe; on stem of *Persea americana* (avocado), possibly causing stem dieback); 16 Oct 1998; V. Herrera, isol. C.F. Hill, SUR 93/6 (CBS 101918). – U.S.A. PENNSYLVANIA: Chester County, woods W of experimental greenhouses, Longwood Gardens, Kennett Square; on dead branches of *Liriodendron tulipifera*; 14 Oct 1978; C.T.R., D.G. Huttleston (NY; C.T.R. isolate 75-207). – VENEZUELA. Edo. Aragua: Parque Nac. Henry Pittier, *ca* 21 km above Maracay, on Maracay–Choroni Rd.; on unidentified wood; 13 Jul 1971; K.P.D., J.H. Haines, G.J.S. (NY; VEN; Dumont-VE 2154). – Ravine, 2.5 km S of Rancho Grande, on Rancho Grande–Maracay Rd.; on unidentified wood; 5 Jul 1971; K.P.D., J.H. Haines, G.J.S. (NY; VEN; Dumont-VE 1374; C.T.R. isolate 71-223). – Edo. Mérida: Parque Nac. Sierra Nevada, above fish hatchery at La Mucuy, 7 km E of Tabay; on unidentified wood; 25 Jul 1971; K.P.D., G.J.S., L. Borjas (NY; VEN; Dumont-VE 2710). – *Ca* 4 km inside San Javier del Valle resort, 7 km NE of Mérida; on unidentified twig; 24 Jul 1971; K.P.D., G.J.S., L. Borjas (NY; Dumont-VE 2858; C.T.R. isolate 71-285). – Edo. Sucre: Trail between Los Pocitos and the peak of Cerro Humo, NW of Irapa; on unidentified wood; 12 Jul 1972; K.P.D., R.F. Cain, G.J.S., G. Morillo, F. Farfan (Ven, NY; Dumont-VE 4831; C.T.R. isolate 72-122, CBS 365.78). – Along Rio Aguas Calientes, 30 min walk N of Maraval, NW of Irapa; on unidentified bark; 8 Jul 1972; K.P.D., R.F. Cain, G.J.S., G. Morillo, A. Villegas (NY; Dumont-VE 4337; C.T.R. isolate 72-95). – Trail between Manacal and Los Pocitos, NW of Irapa; 10 Jul 1972 (NY; Dumont-VE 4615; C.T.R. isolate 72-105). – Edo. Trujillo: Parque Nacional Guaramacal, *ca* 10 km SW of Batatal, La Defensa, along Río Saguás, Campamiento Granja Bocono, in disturbed vegetation along river, 09°19' N, 70°09' W, 2000 m alt.; on bark; 20 Nov 1980; G.J.S., B. Hein, S.M. Huhndorf (B, BPI, NY; G.J.S. 7312, USB, VEN; CBS 216.93,

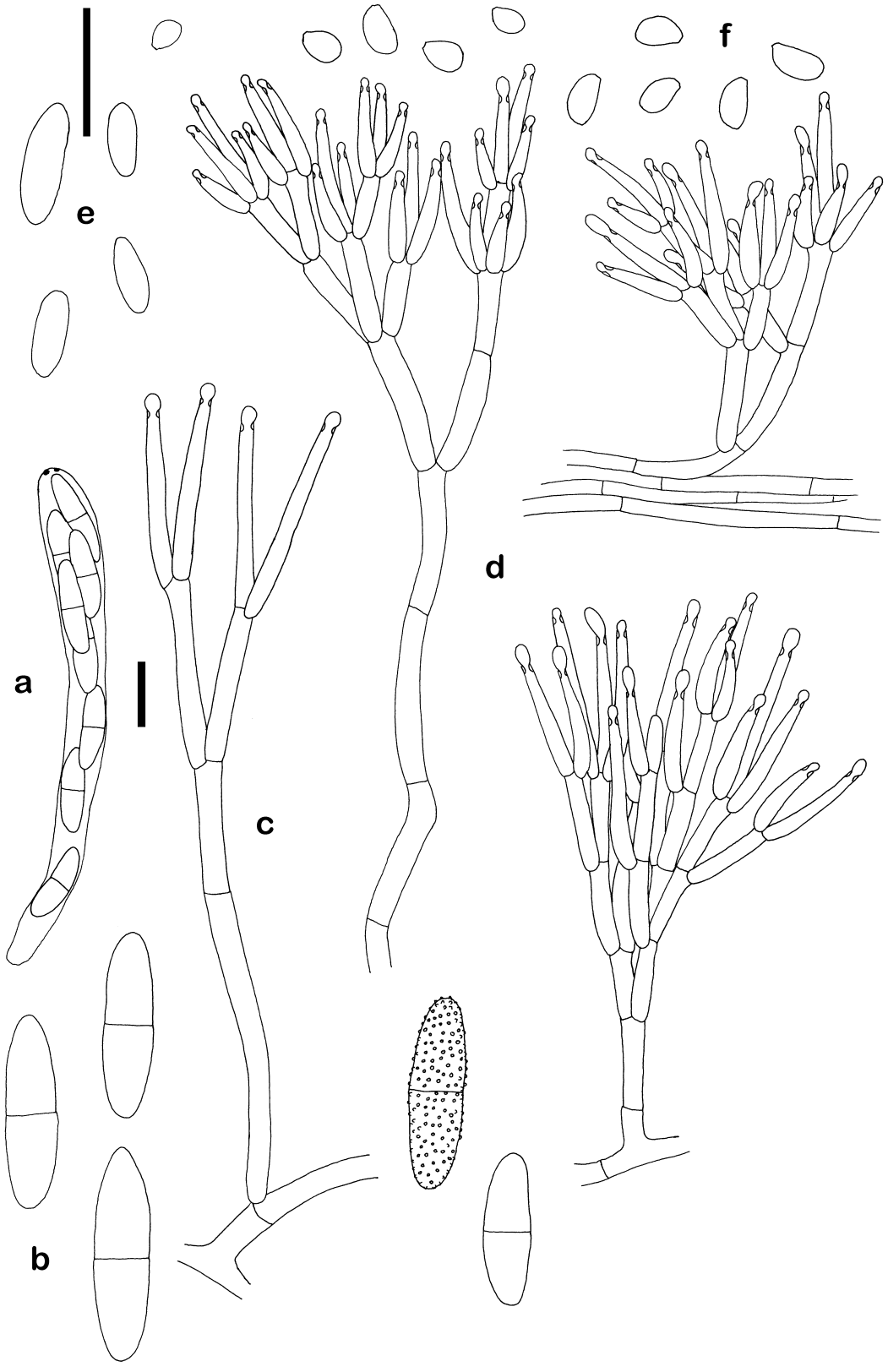


Fig. 19. ***Bionectria byssicola*** **/** ***Clonostachys byssicola*****. a.** Almost mature ascus. **b.** Ascospores. **c.** Side branch of verticillium-like, primary conidiophore arising from lower part of short stipe (main axis not shown), conidia extruding symmetrically from phialides. **d.** Secondary conidiophores; sporodochial aggregate with stipe arising from subhymenium (left), with stipe arising from strand of aerial mycelium (right), with short stipe (bottom), penicillus ± adpressed, main branches somewhat divergent. **e, f.** Conidia, from primary conidiophores (e), from secondary conidiophores (f). – a: Dumont-VE 1708; b: CBS 914.97 (left), CBS 206.93 (right); c–f: CBS 914.97. a, b: natural substratum; c–f: 7–10-d-old OA culture. Scale bars = 10 µm; the shorter bar applies to a, c, d, the longer to b, e, f.

G.J.S. isolate 90-179). – Gauchi, 22 km W of Caño Zancudo, on boundary of Edo. Zulia and Edo. Mérida; on unidentified wood; 22 Jul 1971; K.P.D., G.J.S., L. Borjas (NY; Dumont-VE 2710). – Dto. Fed., *ca* 2 km W of Osma on road between Los Caracas and Todasana; on unidentified wood; 23 Jul 1972; K.P.D., R.F. Cain, G.J.S., B. Manara (NY, VEN; Dumont-VE 5753; C.T.R. isolate 72-143).

Notes: The specimen Thwaites 173 contained several nectrioid species. Berkeley and Broome divided it into several portions, of which they used two as type specimens for *N. byssicola* and *N. subquaternata*. Samuels (1976a) summarized the interpretations of the different portions provided by several scientists. The relevant material and permanent slides were reexamined during this project. The concept of *B. byssicola* presented here conforms to that provided by Samuels (1976a), Samuels *et al*. (1990) and Schroers & Samuels (1997). Some confusion, however, persists in the interpretation of the original material.

Berkeley & Broome (1873) described *N. byssicola* from the portion '173d' (type specimen) as having pale orange, scurfy perithecia and ascospores of 12.5 × 3–4 µm. No such perithecia and ascospores could be found on the specimen 173d (K). Instead, it contained perithecia of *Bionectria subquaternata* (ascospores to 18 µm long, striate) and *Bionectria pityrodes* (ascospores to 28.5 µm long, ± smooth, broadly rounded at ends).

Samuels (1976a) examined two specimens from one sheet, one of which was labelled '173a' (type for *N. subquaternata*, K). Slides of both portions are preserved and contain squash preparations of perithecia that show unevenly thickened walls in the perithecial wart cells and 9–12 × 3.5–4 µm large ascospores. These characters are not indicative for *B. subquaternata* but for *B. byssicola* as it is described here. Contrary to the information derived from the slides, only ascocarps of *B. subquaternata* were seen in '173a'. Samuels (1976a) also prepared sections of a perithecial stroma from Ceylon '173d' (slides in NY) and removed a minute piece from the type specimen which he labelled 'isotype for *N. byssicola* Berk. & Broome' (NY). The 'isotype' consists of two clusters of perithecia from which I examined a small piece of the perithecial wall. The structures were the same as observed in the sections prepared by Samuels, which he labeled 'true *byssicola*'. The perithecia in the 'isotype' are formed on a small erumpent stroma consisting of angular cells, and the perithecial wall consists of angular cells that are partly arranged in chains and have uniformly thickened walls (not shown). These structures are not typical of *B. byssicola*, rare in nectrioid fungi in general but are found for example in *Stilbocrea gracilipes* (Tul. & C. Tul.) Samuels & Seifert. It is therefore possible that the 'isotype' of *B. byssicola* (NY) is an immature specimen of *Stilbocrea gracilipes*. The type specimen of *B. byssicola* [Ceylon 173d (K) and the isotype (NY)] obviously do not contain any perithecia of *B. byssicola* in the sense that is redescribed here but only *B. subquaternata*, *B. pityrodes* (type specimen, K) and *Stilbocrea gracilipes* (NY).

From the original description it is, however, clear that Berkeley & Broome recognized *B. byssicola* as distinct from *B. subquaternata* and *B. pityrodes*. A fungus matching their diagnosis is documented by slides made by Samuels that show the features described here for *B. byssicola* (slide ex '173a', and slide '173 GHKT', NY). Although the perithecia in these slides do not originate from Ceylon 173d (type specimen of *N. byssicola*), they at least do originate from the original specimen 'Ceylon 173', of which Ceylon 173d is a fraction. Because the 'isotype' contains *Stilbocrea gracilipes* and no perithecia of *B. byssicola* remain either on Ceylon 173a or on Ceylon 173d, the slide '173 GHKT' was designated as lectotype for *N. byssicola* by Schroers & Samuels (1997). To support the concept presented in 1997, another tropical specimen was designated by Schroers & Samuels as epitype.

Bionectria byssicola is a very common species in the neotropics. Perithecia can be identified as *B. byssicola* if the warts are well-developed (Fig. 18 b), having cells with unevenly thickened walls (Fig. 18 e–g) and if ascospores are finely warted or only rough (Fig. 18 k). The presence of unevenly thickened walls of the warts is not an unequivocal feature of *B. byssicola*, since they are also formed by *B. ochroleuca*, although not arranged in large perithecial warts (Schroers *et al*., 1999b: Fig. 10), *B. apocyni* (Fig. 8 e), *B. capitata* (Fig. 21 d, e), and others. Although the size range of ascospores may overlap with that of *B. ochroleuca* for example, many specimens have ascospores as long as 19 µm. The anamorph is to a certain degree diagnostic but particularly difficult to distinguish from *B. ochroleuca*. In contrast to *B. ochroleuca* and others, the phialides of the primary conidiophores are generally held at acute angles and side branches arise more frequently from the base of the conidiophore stipe (Fig. 19 c). Secondary conidiophores frequently have short stipes that may merge directly with the hyphae of the aerial mycelium, at least in culture (Fig. 19 d). Such conidiophores are frequently densely aggregated, resulting in small and rather flat sporodochial structures. Conidia formed on secondary, sporodochial conidiophores are frequently very small and some are even not much longer than wide (Fig. 19 f). Columns of imbricate conidia formed on the secondary conidiophores quickly tend to collapse to slimy masses, possibly because of a stronger divergence of the branches and the small size of conidia. In several strains of *B. byssicola*, conidia from primary conidiophores arise symmetrically from the phialide (Fig. 19 c) but I am uncertain if this is an exclusive feature of this species.

7. Clonostachys rhizophaga (Tehon & Jacobs) Schroers, *sp. nov.* — Fig. 20 a–c.

≡ *Verticillium rhizophagum* Tehon & Jacobs, Bulletin of The Davey Tree Expert Company, Kent, Ohio 6: 16. 1936 [Nom. inval. Art. 36 (Greuter *et al*., 2000)].

Clonostachydi roseae similis sed conidiophoris secundariis in vitro raris vel absentibus et ramulis conidiophorum secundariorum divergentibus nec compressis. Conidia (4.8–)5.8–6.4–7(–9) × (2.4–)2.6–3–3.2(–4.2) µm.

Holotypus anamorphosis: herb. CBS; cultura sicca, isolata ex CBS 202.37; cultura viva CBS 202.37.

Teleomorph: Unknown.

Description from culture: **Colonies** reaching 40–50 mm diam in 7 d at 24ºC; optimum for growth (24–)27(–30)°C (55 mm diam), maximum 33°C. Colony reverse on OA and PDA pale to light yellow (4A3–5) after incubation in darkness and under day-light, to light orange (5–6A5) when incubated under UV. Colony surface finely granular because of the conidial masses; aerial mycelium sparsely produced, only formed close to the agar as creeping hyphae or thin hyphal strands; surface unpigmented or like the colony reverse. **Conidiophores** dimorphic. Primary conidiophores verticillium-like, formed throughout the colony and dominating, arising from the agar surface or from the sparse aerial mycelium; sometimes with main side branches arising from the lower part of the stipe; stipe varying in length, sometimes short with side branches arising from the near base, (10–)40–100 µm long, 2.5–5 µm wide at base; penicillus 30–100 µm high; branches and, particularly, phialides divergent; phialides in whorls of 2–5, also singly, particularly when arising from lower levels, straight, slightly tapering towards the tip, with a barely visible collarette, (15.6–)22–28.4–34.2(–48.2) µm long, (2.2–)2.6–2.6–2.6(–3.2) µm wide at base, (1–)1.4–1.6–1.6(–1.6) µm wide near aperture (n = 42), each producing a small, hyaline drop of conidia. Secondary conidiophores penicillate, sparsely formed, inconspicuous and solitary among the primary conidiophores, ter- to quaterverticillate; branches divergent or more or less divergent; phialides in loose apical whorls of 3–5, or from lower levels, divergent or adpressed, mostly straight or slightly curved, cylindrical and slightly tapering towards the tip or narrowly flask-shaped and slightly widening in the lower third, without a visible collarette, (5.8–)12.4–14.6–17.2(–25.2) µm long, (2.2–)2.6–2.6–2.6(–3.2) µm wide at base, (1–)1.2–1.4–1.6(–1.6) µm wide near aperture (n = 57); intercalary phialides sometimes observed. **Conidial masses** on verticillium-like conidiophores in small round collapsing to form whitish, watery masses; conidial masses on penicillate conidiophores inconspicuous, short and rather thick, columnar, white. **Conidia** hyaline or with a greenish hyaline tinge (CBS 529.80), minutely curved, slightly tapering distally, with laterally displaced hilum, (4.8–)5.8–6.4–7(–9) × (2.4–)2.6–3–3.2(–4.2) µm (n = 89). Sporodochia not observed. Perithecia not observed.

Type: U.S.A. OHIO: Dayton; from root of *Ulmus americana*; 2 Oct 1934; L.R. Tehon, No. 21-A-1 (herb. CBS; dried culture ex CBS 202.37, MUCL 8001).

Known distribution: Probably cosmopolitan.

Habitat: Conidia isolated form various kinds of soil, and from roots of *Ulmus americana* and *Pisum sativum*.

Published descriptions and illustrations: Tehon & Jacobs (1936).

Additional specimens/strains examined: CHILE. From meadow soil; J. Grinbergs (CBS 906.72A). – ECUADOR. Form root of *Pisum sativum*; J.P. Laoh (CBS 529.80; masses of conidia with a greenish tinge). – SWITZERLAND. Zürich; culture contaminant; D. Rast, Bot. Inst. Univ. Zürich (CBS 361.77, Rast No. A9). – U.S.A. WASHINGTON: From soil; 1930 (CBS 229.48, ATCC 10521, DSM 1165, IMI 040024, NRRL 1085). – Location unknown: G. Gindrat (G. Gindrat 1-1, NS 36, CBS 100004).

Notes: *Clonostachys rhizophaga* differs slightly from *C. rosea*. Most strains have previously been identified as *Gliocladium roseum*. Primary conidiophores with divergent phialides dominate in the colonies and only a few secondary conidiophores are formed inconspicuously among the verticillium-like conidiophores, or secondary conidiophores were not observed at all. It is possible that the sparse formation of seconddary conidiophores indicates degeneration, because Tehon & Jacobs (1936) described both kinds of conidiophores in the freshly isolated type strain. If formed, the secondary conidiophores of *C. rhizophaga* are more divergently branched than those of *C. rosea* (compare Fig. 20 b with Fig. 16 b) and may be morphologically similar to those found in *B. solani* (Figs 36 c–e, 37 d).

Secondary conidiophores were consistently absent in CBS 529.80. The strain, however, differs from other cited strains in greenish, almost colourless, shades of the conidial masses formed on the verticillium-like conidiophores. Therefore, *C. rhizophaga* might form both greenish and unpigmented to pale orange conidial masses, as is found in *C. rosea* and *C. solani*. The strain CBS 100004 differs from others in *C. rhizophaga* by its more abundantly formed secondary conidiophores that ± entirely form distinct sporodochial aggregates directly on the agar surface and not from aerial hyphae. The abundant formation of secondary conidiophores could mean that this strain is closer to the wild type of the species.

Because of the rather cryptic characters, the recognition of *C. rhizophaga* and the identification of the strains CBS 529.80 and CBS 100004 is mainly based on DNA sequence analyses (Fig. 4 a–c).

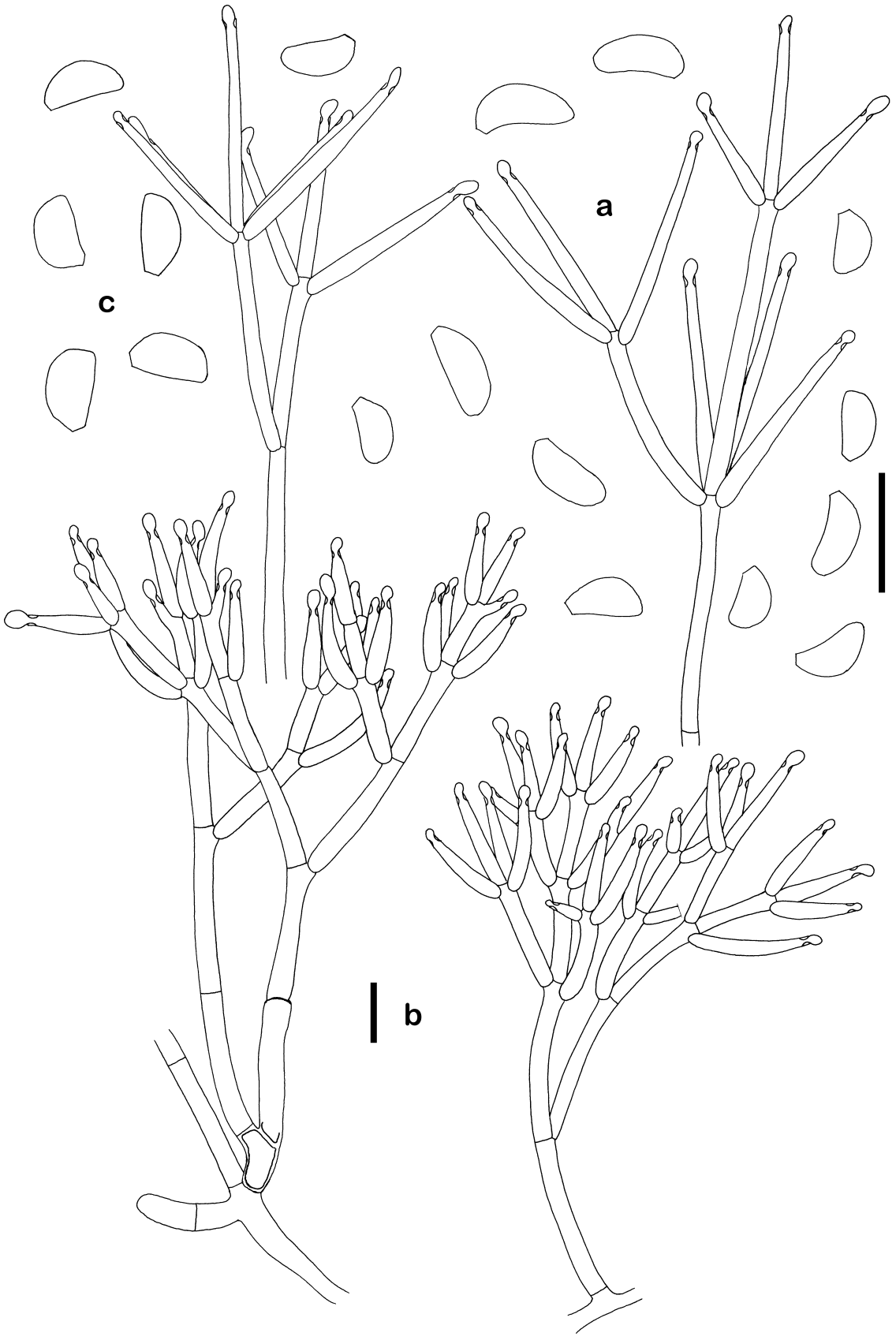


Fig. 20. ***Clonostachys rhizophaga*****. a.** Verticillium-like primary conidiophores. **b.** Rarely observed secondary conidiophores. **c.** Conidia. – a: CBS 202.37 (left), CBS 100004 (right); b: CBS 149.72 (left), 202.37 (right); c: CBS 202.37. – All from 7–10-d-old OA cultures. Scale bars = 10 µm; the shorter bar applies to a, b, the longer to c.

Based on parsimony and maximum likelihood analyses of *tub*2 sequences, *C. rhizophaga* is closely related to *B. byssicola* (Fig. 4 a, c). The more divergent branches of the primary conidiophores separate *C. rhizophaga* from *B. byssicola* (Fig. 20 a, b *vs.* Fig. 19 c, d). Based on cluster analyses (Fig. 4 b), however, *C. rhizophaga* appears closely related to *B. apocyni* and *B. kowhaii*. Because of the size range of the conidia and overall characters of the conidiophores, its close relationship to *B. byssicola* is considered more likely.

Tehon & Jacobs (1936) reported a disastrous disease of *Ulmus americana* caused by *C. rhizophaga* in the original description of the species. Following their report, the trees died after a period of wilting, obviously caused by disintegrating phloem and cambium in the plant roots. Tehon & Jacobs also reported similar disease symptoms in young trees grown in sterile soil that was inoculated by *C. rhizophaga*. However, to my knowledge, such a tree disease has not been linked again to *C. rhizophaga* or another species in *Clonostachys*. In fact, the disease of the elms possibly was caused by *Ophiostoma ulmi* or *O. novo-ulmi* and it could be that the *Clonostachys* secondarily invaded the dying trees (K.A. Seifert, pers. comm.).

Beside the ex-type strain preserved at CBS, no material, particularly no dried specimen could be located of *V. rhizophagum*. The original description includes both kinds of conidiophores with details indistinguishable from the diagnosis provided here. Therefore there is little doubt about the authenticity of the ex-type strain. The species is invalidly described because no Latin diagnosis was included (Tehon & Jacobs, 1936). A dried strain derived from the original strain is here designated as the neotype of the species.

8. Bionectria capitata Schroers & Samuels, *sp. nov.* — Figs 21 a–i, 22 a, b.

Anamorph: ***Clonostachys capitata*** Schroers, *stat. nov.* — Figs 21 j, k, 22 c–e.

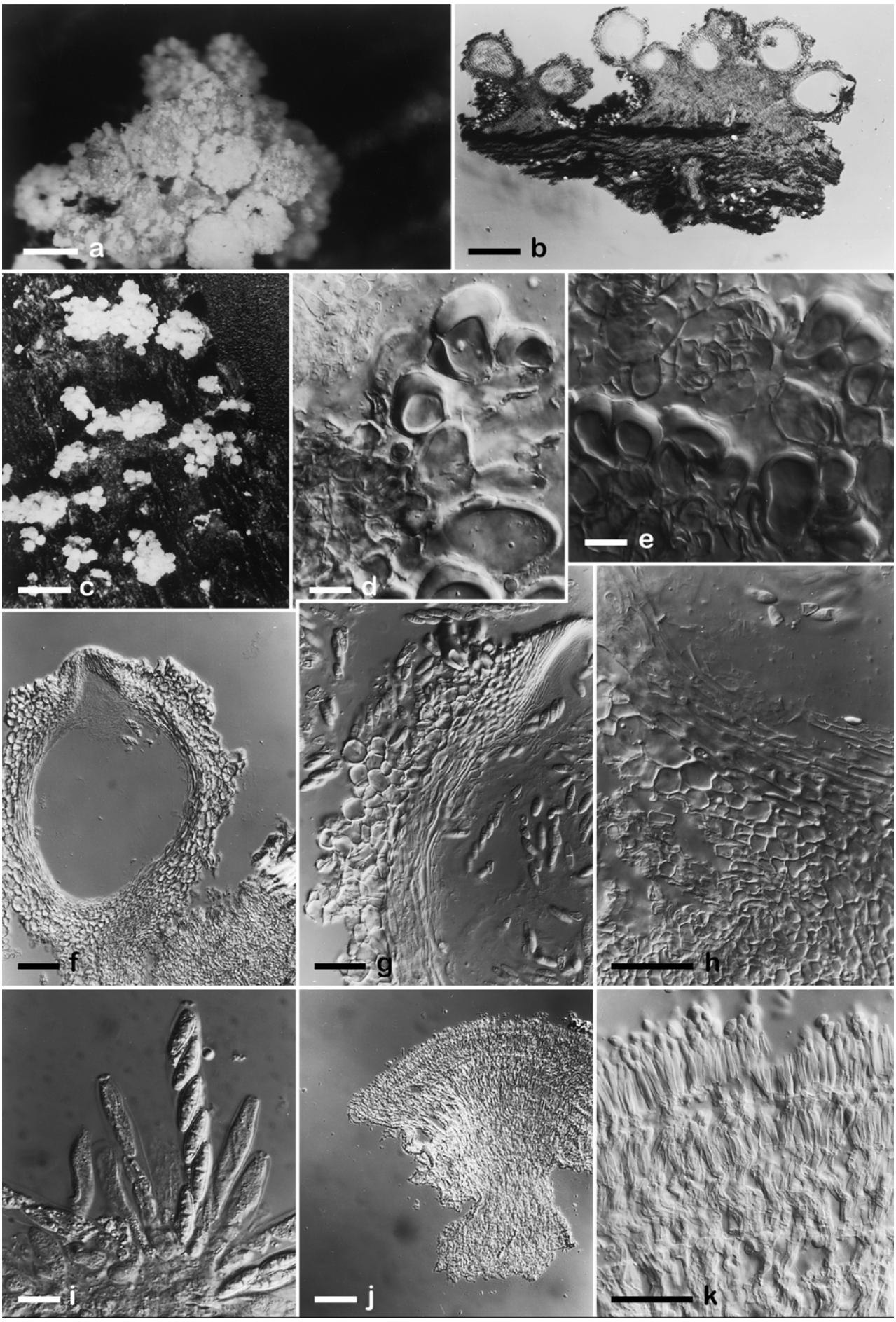
Bionectriae byssicolae similis sed paries peritheciorum strato medio deficiens. *Bionectriae zelandiaenovae* similis sed cellulis strati exterioris et verrucis peritheciorum extus crassitunicatis. Ascosporae (11.6–)13.8–14.8–15.6(–18.8) × (3.6–)4.2–4.8–5 (–5.8) µm. Anamorphosis *Clonostachys capitata*. Conidiophoris dimorphoricis. *Clonostachydi roseae* et C. *byssicolae* similis. Conidiis vulgo majoribus, (4.6–)6–6.8–7.2(–12.4) × (2.2–) 2.8–3.2–3.4(–4.2) µm.

Holotypus teleomorphosis: Specimen PDD 46486. Holotypus anamorphosis: PDD; cultura sicca, isolata ex specimine PDD 46486; isotypus herb. CBS; cultura viva CBS 218.93.

Etymology: Latin *capitatus* 'with a knob-like head or tip', referring to the cells composing the perithecial warts showing unevenly thickened walls.

Description from natural substratum: Stroma well-developed, erumpent through bark, bearing sporodochia or perithecia, sometimes on or next to the stroma of other pyrenomycetes; cells angular to subglobose. **Perithecia** in crowded groups of 5–30, subglobose to oval, around 300 µm diam, not markedly pinched when dry, pale to brownish orange, minutely papillate, with a somewhat more pigmented ostiolar region, with a warted surface. **Perithecial warts** off-white to yellowish white, to 40 µm high and 100 µm diam; cells angular to globose, (9–)12.5–20 (–31) × (6–)9.5–13 (–23) µm, with unevenly thickened walls up to 17.5 µm thick. **Perithecial wall** 45–60 µm thick, composed of two regions. Outer region 20–30 µm or to 3 cells thick; cells angular to globose, (8–)12–15–18(–27) × (5.5–)8.5–10.5–13(–17.5) µm, with uniformly thickened walls up to 2 µm thick; vacuoles not observed. Hyphal layer (middle region) not observed. Inner region 20–30 µm thick. **Asci** narrowly clavate, (50.5–) 62.5–66.5–72(–89.5) × (7–)8.5–9.5–10.5(–12) µm (n = 56), 8-spored; apex rounded, ring clearly visible. **Ascospores** ellipsoidal to oblong-ellipsoidal, spinulose to warted, colourless, (11.6–)13.8–14.8–15.6(–18.8) × (3.6–)4.2–4.8–5(–5.8) µm (n = 88). **Sterile mycelium** generally not formed on the substratum. **Sporodochia** frequently close to the perithecial clusters; branches of conidiophores and phialides forming in a *textura porrecta*.

Description from culture: Colonies reaching 30 mm in 7 d at 24ºC; optimum for growth 24–27°C, maximum 33°C. Colony reverse on OA and PDA pale yellow (4A3), pale orange after incubation under UV. Colony surface finely to coarsely granular because of the sporodochia and confluent conidial masses or exudates, or felty to cottony because of the strands of aerial mycelium; surface unpigmented or with pale orange granules because of the conidial masses. **Co-**


a
b
c
d
e
f
g
h
i
j
k

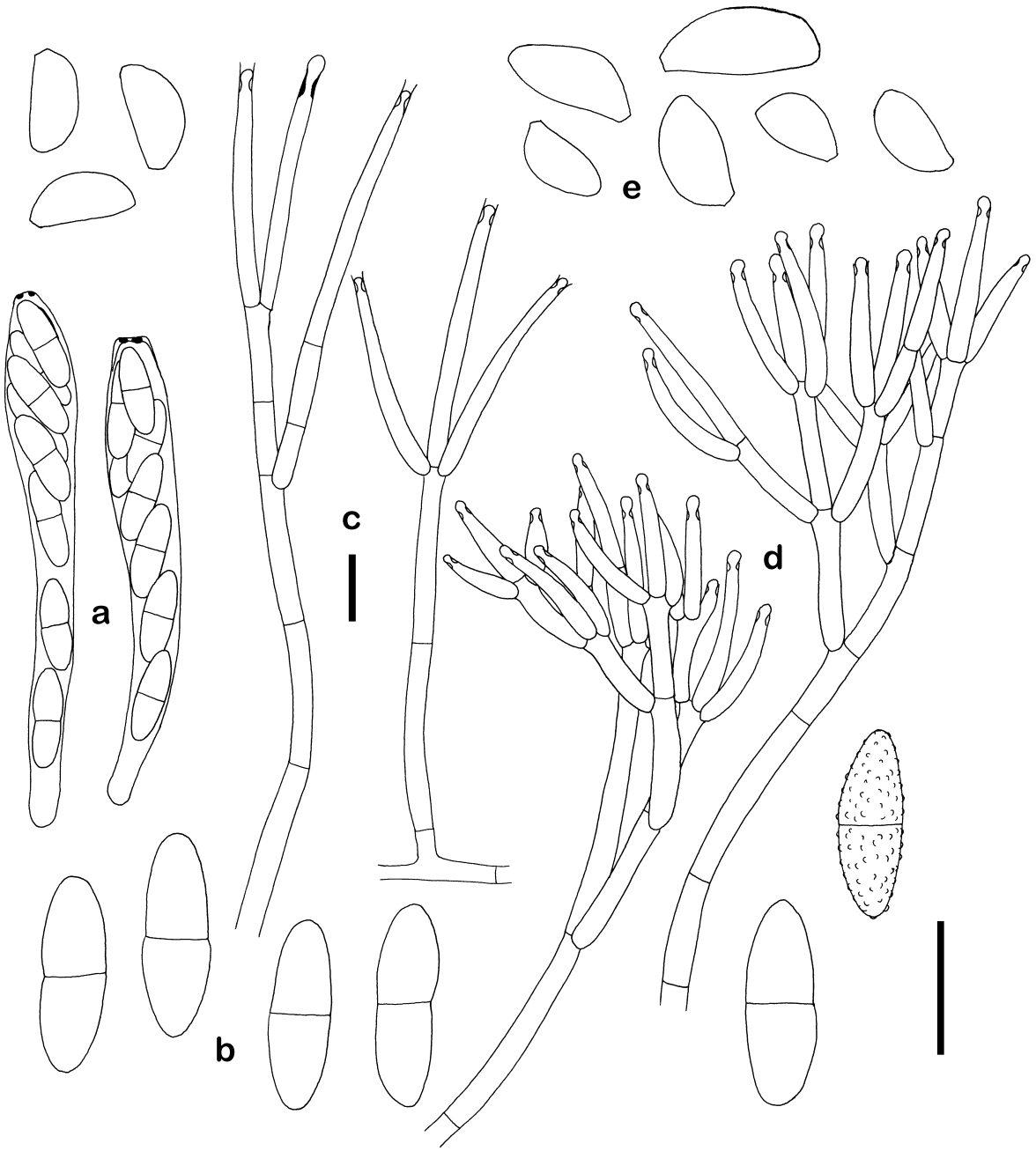


Fig. 22. ***Bionectria capitata*** **/** ***Clonostachys capitata*****. a.** Almost mature asci. **b.** Discharged ascospores. **c.** Verticillium-like primary conidiophores, sparsely branched. **d.** Secondary conidiophores from sporodochial cluster with adpressed or somewhat divergent branches and phialides. **e.** Conidia. – a (left), b, d (right): PDD 46486 (CBS 218.93); a (right), c (right): PDD 46522 (G.J.S. 83-340); c (left), d (left): G.J.S. 83-335; e: CBS 218.93. a, b: natural substratum; d (right), e: 10-d-old OA culture; others: dried culture. Scale bars = 10 µm; the shorter bar applies to a, c, d, the longer to b, e.

nidiophores dimorphic. Primary conidiophores verticillium-like, formed throughout the colony, dominating towards the margin, arising from the agar surface or from aerial hyphae, rather infrequently branched; phialides divergent at more or less acute angles; stipes rather longer than the branching part, to 100 µm long and to 3.5 µm wide at base; phialides in whorls of 2–4, straight, cylindrical, slightly tapering towards the tip, with a minute collarette, (18.6–)28.4–33.8–40.2(–46.6) µm long, (1.4–)2–2.2–2.4(–2.6) µm wide at base, (1.4–)

Fig. 21. ***Bionectria capitata*** **/** ***Clonostachys capitata*****. a, c.** Habit of crowded perithecia. **b, f–h.** Sections through perithecia and stroma, lateral perithecial wall (g) with perithecial warts; middle, hyphal region lacking, cells of stroma merging with those of the outer perithecial wall (h). **d, e.** Surface cells of perithecial wall in squash preparation with unevenly thickened walls. **i.** Almost mature ascus, apical ring visible. **j, k.** Sections through sporodochium with subhymenium and phialides arranged in *textura porrecta*. – a, c, d, j, k: PDD 46522; b, f–h, i: PDD 46486; e: PDD 46518. All from natural substratum. a, c: DM; b: LM; d–k = DIC. Scale bars: a = 200 µm; b = 250 µm; c = 1250 µm; d, e, i = 10 µm; f = 50 µm; g, h, k = 30 µm; j = 100 µm.

1.6–1.8–1.8(–2) µm wide near aperture (n = 15), each producing a small, hyaline drop of conidia. Secondary conidiophores ter- to quinquiesverticillate, aggregated in pustules or sporodochia on the agar surface or on strands of aerial mycelium; branches ± adpressed; metulae 9–20 × 3 µm (n = 26); phialides adpressed or slightly divergent, in loose whorls of 3–5, straight to slightly curved, narrowly flask-shaped, generally with widest point in the lower third, or almost cylindrical, but generally slightly tapering in the upper part, without a visible collarette, (8.8–)11.6–13.6–15(–24) µm long, (1.6–)2–2.4–2.6(–3) µm wide at base, (1.8–)2.6–2.8–3(–3.6) µm at widest point, (1–)1.4–1.6–1.6(–2) µm wide near aperture (n = 75). Intercalary phialides rare, solitary, with an up to 7 µm long lateral neck, normally arising below a whorl of terminal phialides. **Conidial masses** white to pale orange, in short imbricate chains or sliming down on sporodochia. **Conidia** hyaline, curved, with broadly rounded ends, with a laterally displaced hilum, (4.6–)6–6.8–7.2(–12.4) × (2.2–)2.8–3.2–3.4(–4.2) µm (n = 152). Perithecia not formed.

Type for *Bionectria capitata*: JAPAN. Gunma Prefecture, Marunuma-ko, on bark of indet. tree; 20 Aug 1983; R.P. Korf (PDD 46486; G.J.S. isolate 83-303, CBS 218.93, ex ascospores). **Type for *Clonostachys capitata*:** dried culture ex CBS 218.93, filed together with type of *B. capitata* (PDD 46486); isotype: herb. CBS.

Known distribution: Japan.

Habitat: On bark of trees, sometimes on conifers.

Additional specimens/strains examined: JAPAN. Honshu: Mt. Fuji, Yoshida-guchi, Nakano-Chaya, 1100–1200 m alt.; on *Abies* sp.; 6 Sept 1983; G.J.S. (PDD 46527, G.J.S. isolate 83-352, dead). – Katashina-Mura, Tone-gun, Jugo Seishi Co. Forest; on bark; 26 Aug 1983; Samuels (PDD 46518; G.J.S. isolate 83-335). – Katashina-Mura, Tone-gun, Jugo Seishi Co. Forest; on conifer; P.F. Cannon (PDD 46522; G.J.S. isolate 83-340, dead).

Notes: *Bionectria capitata* is characterized by relatively large ascospores, cells with unevenly thickened walls composing the perithecial warts (Fig. 21 d, e), and a perithecial wall consisting of only two wall regions (Fig. 21 g, h); so far it is only known from Japan. Formation of only two wall regions contrasts with most other species of subgenus *Bionectria*. In this regard, *B. capitata* resembles the type specimen of *B. tonduzii* and some specimens of *B. apocyni*. The species is otherwise similar to *B. byssicola* and *B. zelandiaenovae* (all having ascospores of a similar range) and warted perithecia. *Bionectria byssicola*, however, has smaller cells in the warts and the walls of the outermost cells in *B. zelandiaenovae* are generally uniformly thick. Secondary conidiophores are solitary only in relatively young colonies and have a strong tendency to form sporodochial aggregates in culture. The conidia formed on secondary conidiophores were found relatively large (Fig. 22 e). The distinctness of this species from other species with dimorphic conidiophores, and particularly from *B. byssicola*, is confirmed by DNA sequences (Figs 2–4).

9. Clonostachys agrawalii (Kushwaha) Schroers, *comb. nov.* — Fig. 23 a–c.

≡ *Gliocladium agrawalii* Kushwaha, Curr. Sci. 49: 74. 1980.

Teleomorph: Unknown.

Description from culture: Colonies reaching *ca* 40 mm diam in 7 d at 24ºC; optimum for growth (24–)27(–30)°C [(42–)48(–43) mm diam], maximum 33°C. Colony reverse on OA and PDA yellowish white to light yellow (4A2–5), not pigmented on CMD after incubation in darkness or daylight/darkness; generally in orange hues (5A2–5) after incubation under UV. Colony surface felty to tomentose to granulose because of the conidial masses; aerial mycelium scanty, on OA forming thin strands, on CMD almost absent except for some creeping hyphae from which conidiophores arise. **Conidiophores** dimorphic. Primary conidiophores (OA) arising from the agar surface or from strands of the aerial mycelium, irregularly branched, with several whorls of phialides along the main axis, to terverticillate; short side branches frequently arising from the lower part or even the base of the conidiophore; branches including the phialides more or less divergent; stipe 10–60 µm long or more, to 4 µm wide at the base; branching part to 100 µm high; phialides in whorls of 2–4, or arising singly from lower levels, straight, almost cylindrical, slightly tapering towards the tip, with a short collarette, 18.8–32–42 µm long, 2.2–2.6–3.0 µm wide at base, 1.4–1.6 µm wide near aperture. Secondary conidiophores (OA) scattered on mycelium near the agar surface, strands of aerial mycelium, or in non-sporodochial aggregates, bi- to quaterverticillate, with somewhat divergent branches; stipe mostly short, shorter than the height of the penicillus; phialides almost adpressed, or divergent at acute angles, in whorls of 3–5, straight to slightly curved, flask-shaped with widest point in the lower third, or almost cylindrical, but generally slightly tapering towards the apex, without a visible collarette, 7–18.2 µm long, 2.2–3 µm wide at base, 2.6–3.4 µm at widest point, around 1.4–1.6 µm wide near aperture (n = 16); conidial masses small dome-shaped or inconspicuously columnar; those on aggregated secondary conidiophores in light yellow to light orange shades. Intercalary phialides rather frequent, solitary, forming a lateral neck below a solitary terminal phialide

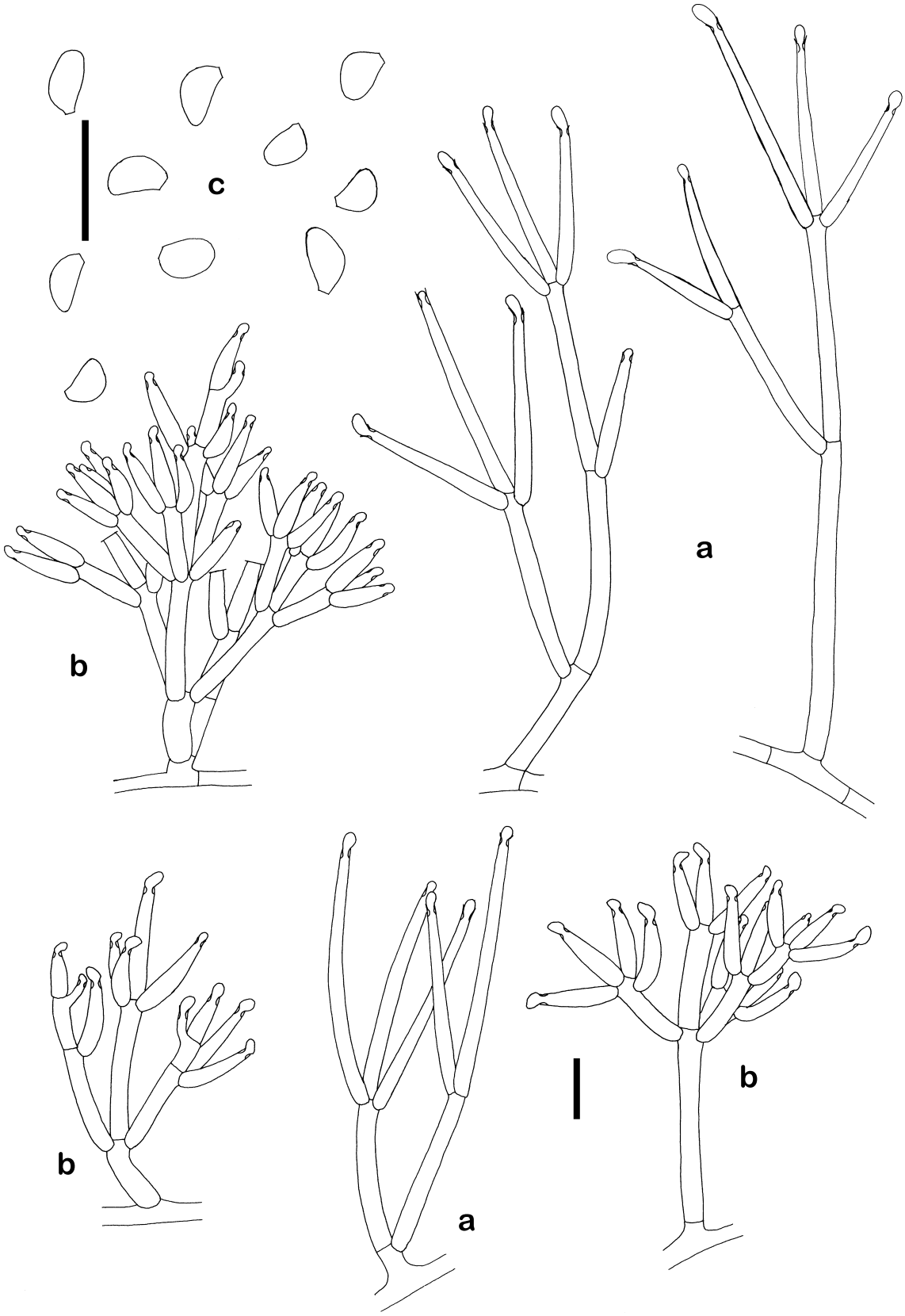


Fig. 23. ***Clonostachys agrawalii*****. a.** Primary verticillium-like conidiophore. **b.** Secondary conidiophores with short stipes, primary branches mostly divergent, rarely with intercalary phialides. **c.** Conidia, slightly curved with one flattened side and laterally displaced hilum. – All: 7–10-d-old OA cultures of CBS 533.81. Scale bars = 10 µm; the shorter bar applies to a, b, the longer to c.

or a whorl of terminal phialides, to 5 µm long. **Conidia** hyaline,minutely curved, ends broadly rounded, with slightly laterally displaced hilum, (3.8–)4.2–4.6–4.8(–5.8) × (2.2–)2.4–2.6–2.9(–3) µm (n = 22). **Perithecia** not observed.

Type for *Gliocladium agrawalii*: The numbers given in the original description, SU/KU 128 (Mycological Collection of Botany Department of University of Saugar) and IMI 179846, refer to living cultures. Neither dried nor living material exists at CABI that relates to IMI 179846 (J. David, pers. comm.). A strain, ITCC 1889, was sent to CBS containing the same information as given in the original description. There is no doubt that this strain originated from the material described. Of the strain retained at CBS, CBS 533.81, a culture was dried and designated as neotype. **Neotype:** Herb. CBS, dried culture ex CBS 533.81.

Known distribution: India.

Habitat: Isolated from decomposing buffalo horn pieces from animal house floor sweepings; habit suggests keratinolytic activities (Kushwaha, 1980).

Published description and illustration: Kushwaha (1980), including remarks on physiological data.

Additional strain examined (identification uncertain): PAPUA-NEW GUINEA. Madang, Jais Aben; from soil along coral reef coast; Nov 1995; A. Aptroot (CBS 196.96).

Notes: *Clonostachys agrawalii* is characterized by relatively short stipes both in the primary and the secondary conidiophores (Fig. 23 a, b). Branches and phialides of the primary conidiophore diverge; phialides diverge at narrow angles or may even be adpressed (see also Kushwaha, 1980: Fig. 1A). Secondary conidiophores in *C. agrawalii* may be less conspicuously formed than in other species of *Clonostachys* and were not described in the original description, although Kushwaha (1980) compared the fungus with *Gliocladium roseum*. Intercalary phialides were frequently found in the penicillate conidiophores. Because they are frequently located below solitary terminal phialides, the intercalary phialides are similar to those found in subgen *Epiphloea* and *Uniparietina* (anamorphs sesquicillium-like). *Clonostachys agrawalii* is only known from a single strain and the ranges of phenotypic variations are unknown. The distinctness of *C. agrawalii* is, however, supported by DNA sequence analyses (Figs 2–4). The species was elsewhere considered a synonym of *Gliocladium roseum* Bain. (= *C. rosea*) (Domsch *et al*., 1980).

10. *Bionectria sporodochialis* Schroers, *sp. nov*. — Figs 24 a–i, 25 a–d, 26 a, b.

Anamorph: ***Clonostachys sporodochialis*** Schroers, *stat. nov*. — Figs 25e–g, 26 c–h.

Bionectriae ochroleucae similis sed peritheciis verrucis brevibus ornatis; *B. byssicolae* similis sed cellulis strati exterioris peritheciorum et verrucae peritheciorum uniformiter tenuitunicatis. Ascosporis (7.8–)9.6–10.4–11(–13) × (2.6–)3.2–3.6–3.8(–5) µm. Anamorphosis omnino sporodochialis vel raro conidiophora primaria divergentia formans. Conidiophora secundaria *C. byssicolae* similia sed phialidibus longioribus, (13.4–)18.8–21.6–24.6(–35.4) µm. Conidia (3.2–)4.4–4.8–5.4(–6.8) × (1.6–)2.0–2.2–2.2(–2.6) µm.

Holotypus teleomorphosis: BPI 748341. Holotypus anamorphosis: BPI; cultura sicca, isolata ex specimine BPI 748341; isotypus herb. CBS; cultura viva CBS 101921.

Etymology: *Sporodochialis*, referring to the sporodochial anamorph.

Description from natural substratum: Stroma well-developed, erumpent through bark, bearing perithecia or sporodochia; cells angular, forming a *textura angularis*. **Perithecia** crowded in groups of up to 50, globose to subglobose, slightly higher than wide, 230–370 µm high, 180–290 µm diam, pinching not observed, yellowish orange, minutely papillate or not, with a somewhat darker contrasting ostiolar region, with rough to warted surface. **Perithecial warts** tan or non-pigmented, rarely yellowish, inconspicuous (perithecia scaly) or well-developed; cells typically subglobose to globose, exceptionally angular, merging with the cells of the outer perithecial wall region, with uniformly thickened walls up to 1.5 µm thick, sometimes arranged in small chains of 2–4. **Perithecial wall** 35–45 µm thick, composed of three regions. Outermost region *ca* 25 µm or up to 5 cells thick; cells angular to subglobose, 4.5–12 × 3.5–9.5 µm (n = 56), with uniformly thickened walls around 1 µm thick, frequently containing a vacuole, or a crystal-like structure. Middle region inconspicuous, 5–11 µm thick. Inner region 10–13 µm thick. **Asci** clavate to narrowly clavate, (45–)54–62–69(–85) × (5.5–)7–8–8.5(–12.5) µm (n = 41); ascus apex broadly rounded, exceptionally flat, ring typically invisible. **Ascospores** ellipsoidal to broadly ellipsoidal, conspicuously warted, colourless, (7.8–)9.6–10.4–11(–13) × (2.6–)3.2–3.6–3.8(–5) µm (n = 210). **Sterile mycelium** invisible. **Sporodochia** frequently associated with the perithecia.

Description from culture: Colonies reaching on CMD 35–40, on OA 40–45 mm diam in 7 d at 24ºC; optimum for growth 24°C (42 mm diam), maximum 30°C. Colony reverse on OA and PDA pale yellow (4A2–3) after incubation in darkness or daylight, to light orange (5A5) under UV. Colony surface on OA and CMA white, finely cottony because of the aerial

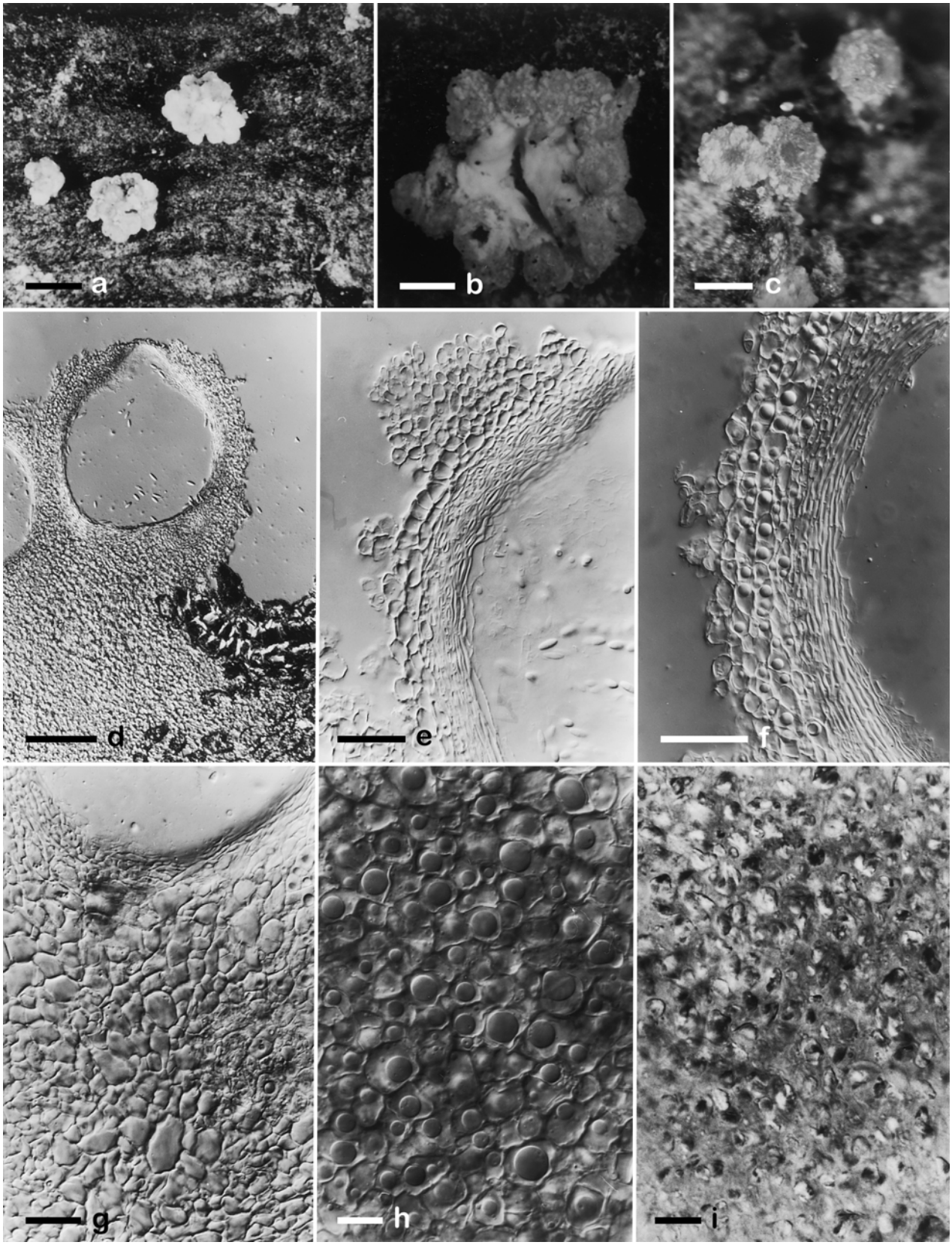


Fig. 24. ***Bionectria sporodochialis*****. a–c.** Habit of crowded, warted perithecia with sporodochial remnants (b). **d–g.** Sections through perithecia and stroma; lateral perithecial wall and perithecial warts (e); lateral perithecial wall (f); stroma below a perithecium (g). **h.** Subsurface view of outer perithecial wall region, cells containing droplets. **i.** Outermost cell layer containing crystal-like structures. – a, b, d, f, g: G.J.S. 7760; c, e, h: G.J.S. 4518; i: BPI 748341. All from natural substratum. a–c: DM; d–i: DIC. Scale bars: a = 750 µm; b = 300 µm; c = 200 µm; d = 100 µm; e–g = 30 mm; h, i = 10 µm.

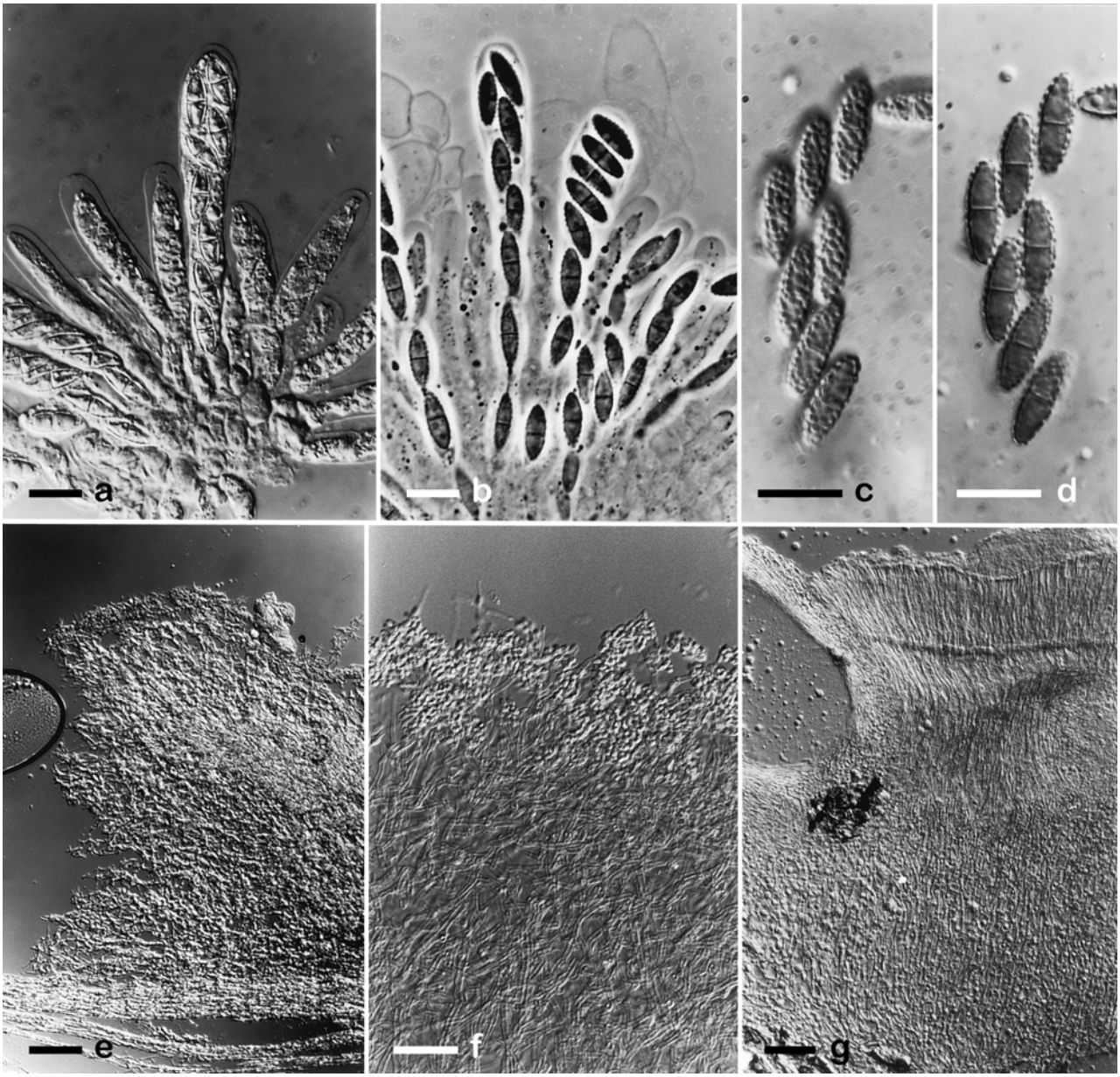


Fig. 25. ***Bionectria sporodochialis*** **/** ***Clonostachys sporodochialis*****. a, b.** Almost mature asci; apex broadly rounded, apical ring invisible. **c, d.** Ascospores in surface view (c) and optical section (d). **e–g.** Sections through sporodochia; with interwoven hyphae if formed in culture (e, f), with parallel hyphae on the natural substratum formed next to perithecia (g). a, b, e, g: G.J.S. 7760; c, d: G.J.S. 5063. f: G.J.S. 4518 (G.J.S. 86-335). a–d, g: natural substratum; e: dried culture; f: 10-d-old OA culture. a, c–g: DIC; b: PC. Scale bars: a–d = 10 µm; e = 100 µm; f = 30 µm; g = 50 µm.

mycelium, or granulose because of sporodochial pustules that later develop into large, robust sporodochia; sporodochial tufts arranged in concentric rings or irregularly scattered, decreasing in size towards the colony margin, frequently forming a large watery drop (exudate) or covered by slimy conidial masses. **Conidiophores** monomorphic or dimorphic; primary conidiophores if present divergently branched (not shown); secondary conidiophores sporodochial to synnematous, penicillate, ter- to quaterverticillate; branches of conidiophores in young sporodochial pustules divergent, in developed sporodochia adpressed; penicillus of conidiophores in young sporodochial pustules 50–120 µm high, 50–100 µm broad; phialides in apical whorls of 2–4, also arising from lower levels, slightly divergent or almost adpressed, straight, hardly narrowing towards the tip, almost cylindrical, without a visible collarette, (13.4–)18.8–21.6–24.6(–35.4) µm long, (1.6–)1.8–2–2.2(–2.6) µm wide at base, (0.8–)1–1.2–1.4(–1.6) µm wide near aperture (n = 79) (phialides of strain CBS 205.93 shorter, (7.7–)9.5–12.7–15.1(–20.2) µm, more strongly divergent). **Conidial masses** on young sporodochial pustules white, forming imbricate columns of conidia, on developed sporodochia pale to light orange; imbricate columns gradually collapsing into slimy masses. **Conidia** hyaline, minutely curved, distally broadly rounded, with laterally displaced hilum, (3.2–)4.4–4.8–5.4(–6.8) × (1.6–)2.0–2.2–2.2(–2.6) µm (n = 164). **Conidiomata** sporodochial to synnematous, with height : width ratio

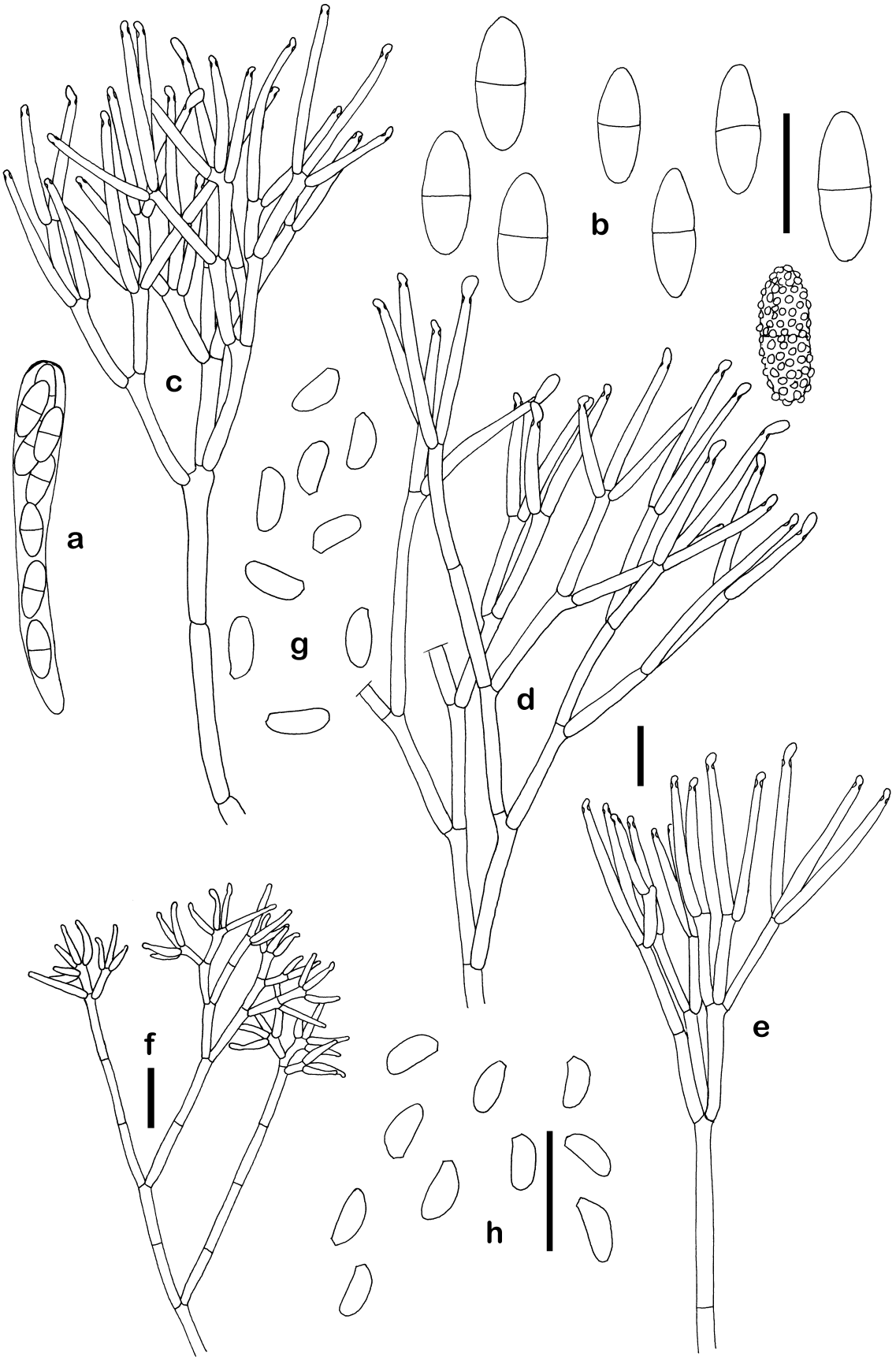


Fig. 26. ***Bionectria sporodochialis*** **/** ***Clonostachys sporodochialis*****. a.** Almost mature ascus. **b.** Discharged ascospores. **c–f.** Conidiophores from young sporodochial aggregates; phialides relatively long, somewhat divergent (c–e), phialides shorter and more strongly divergent (f). **g, h.** Conidia from sporodochia. – a: G.J.S. 7786; b: G.J.S. 7786, BPI 748341, G.J.S. 7760 (CBS 192.93), left to right; c: CBS 101921; d, e CBS 192.93; f: G.J.S. 86-335; g: G.J.S. 86-335; h: CBS 101921. a, b: natural substratum; c–e, g, h: 7-d-old OA culture; f: 14-d-old CMD culture. Scale bar in f = 20 µm; others = 10 µm; the shorter bar applies to a, c–f, the longer to b, g, h.

of 1:1 to 7:1, increasing in width in the upper part, easily removed from agar surface; base soft, composed of irregularly, loosely interwoven hyphae or, in older sporodochia, somewhat gelatinous; hyphae of subhymenium loosely intertwined, in old sporodochia densely packed, forming a *textura porrecta*. **Perithecia** not observed in culture.

Type of *Bionectria sporodochialis*: U.S.A. PUERTO RICO: Caribbean National Forest, Luquillo Mts., Veredia El Toro; on bark of recently dead branches; 24 Feb 1996; H.-J. Schroers 0126, G.J.S., D.J. Lodge (BPI 748341; ex-type strain: CBS 101921, derived from ascospores of BPI 748341). **Type of *Clonostachys sporodochialis*:** dried culture ex CBS 101921, filed together with type of *B. sporodochialis* (BPI 748341); isotype: herb. CBS.

Known distribution: The neotropics: Venezuela, Guyana, French Guiana, U.S.A. (Puerto Rico).

Habitat: On bark of recently dead woody plants.

Additional specimens/strains examined: COLOMBIA. Dpto. Boyacá: *Ca* 21 km from Aguazul, on the Aguazul–Sogamoso Rd., *ca* 820 m alt.; on indet. vine; 14 Jun. 1976; K.P.D., S.E. Carpenter, M.A. Sherwood, L.A. Molina (NY; Dumont-CO 5269). – FRENCH GUIANA. Saül, *ca* 15 km SW of Saül (03°60' N, 53°20' W), toward Mt. Galbao, 03°50' N, 53°20' W, 600–650 m alt.; on vine; Jan 1980; G.J.S., J.R. Boise (NY; G.J.S. 3112). – GUYANA. Headwaters of Kangu River, W branch, *ca* 4 km NW of eastern peak of Mt. Ayanganna, first talus slope on sandstone, 05°25' N, 60°30' W, *ca* 700 m alt.; on branchlets of recently dead tree; 5–7 Mar 1987; G.J.S., J. Pipoly, G. Gharbarran, J. Chin, R. Edwards (BPI, NY; G.J.S. 5063). – Base of Mt. Wokomung, *ca* 5.5 h walk NE of Kopinang Village at base of Mt. Wokomung in legume-dominated forest, 05°05' N, 59°49' W, *ca* 720 m alt.; on bark of recently dead tree; 27 Jun 1989; G.J.S., B.M. Boom, G. Bacchus (NY; G.J.S. 6254A; G.J.S. isolate 89-46). – U.S.A. PUERTO RICO: Caribbean National Forest, Luquillo Mts., El Verde Research Area, La Prieta Creek; 20 Feb 1996; G.J.S., H.-J. Schroers, D.J. Lodge (BPI, H.J.S. 56). – Luquillo Mts., Bisley Experimental Watershed; on bark of recently dead mango tree; 21 Feb 1996; G.J.S., H.-J. Schroers, D.J. Lodge (BPI, H.J.S. 82). – Luquillo Mts., trail to Cocle Falls from Rout 191; on bark of recently dead tree; 23 Feb 1996; G.J.S., H.-J. Schroers (BPI, H.J.S. 111). – Luquillo Mts., Veredia El Toro; on bark of recently dead tree; 24 Feb 1996; G.J.S., H.-J. Schroers, D.J. Lodge (BPI, H.J.S. 114). – Reserva Forestal Toro Negro, along trail beside stream of watershed of Salto Inabón, from Hwy 143 at km 18.6 at Monte Jayuya, *ca* 18°10' N, 66°38' W, 1210–1265 m alt.; 9 Jan 1992; R.C. Harris 27341 (NY). – VENEZUELA. Edo. Aragua: Parque Nac. Henri Pittier, vic. Rancho Grande Biological Station, trail between El Portachuelo and Pico Periquito, 10°21' N, 67°41' W, 1200–1400 m alt.; on woody vine; 2 Dec 1990, G.J.S., B. Hein, S.M. Huhndorf, A. Ortega (BPI, NY; G.J.S. 7786; G.J.S. isolate 90-186). – Ibid.; on branchlets of recently dead tree; 2 Dec 1990, G.J.S., B. Hein, S.M. Huhndorf, A. Ortega (BPI, NY, VEN; G.J.S. 7760; CBS 192.93, G.J.S. isolate 90-192). – 8.6 km S of Rancho Grande on Rancho Grande–Maracay road, Parque Nac. Henry Pittier; on unidentified wood; 6 Jul 1971; K.P.D., J.H. Haines, G.J.S. (NY; Dumont-VE 1445). – Edo. Bolivar: Km 110–111 S of El Dorado, on road between El Dorado and Sta. Elena; on small unidentified dead tree; 6 Aug 1972; K.P.D., R.F. Cain, G.J.S., C. Blanco (NY; Dumont-VE 7127; C.T.R. isolate 72-192).

Notes: *Bionectria sporodochialis* is characterized by its almost entirely sporodochial anamorph. Verticillium-like primary conidiophores were rarely seen and are possibly absent after subculturing. The sporodochia in culture are frequently higher than wide, sometimes appear synnematous, and have loosely, intricately arranged hyphae in the subhymenium (Fig. 25 e, f); those formed on the natural substratum may have a subhymenium of densely aggregated conidiophores that form a *textura porrecta* (Fig. 25 g). The phialides in *B. sporodochialis* are longer than those of the secondary conidiophores in other species (Fig. 26 c–e). The teleomorph is recognizable by a combination of inconspicuous characters such as rather yellowish to pale orange perithecia, relatively small, sometimes yellow perithecial warts consisting of subglobose cells with uniformly thin walls (Fig. 24 e), lack of an ascal ring (Fig. 25 a, b) in most, but not all observed specimens, and 'crystal-like structures' inside the cells of the outer wall region (Fig. 24 i), which were found in several specimens.

The relatedness of *B. sporodochialis* to species of subgenus *Bionectria* is indicated by ascospore morphology (Fig. 25 c, d), the shape of the conidia (Fig. 26 g, h), and sequence data (Figs 2–4). Its relatedness to the species of the core group of subgenus *Bionectria* (Fig. 4 a–c: P) is supported by the infrequent presence of a verticillium-like primary conidiophore (not shown).

The specimen G.J.S. 4518 (CBS 205.93) could not be distinguished from other specimens of *B. sporodochialis* in perithecial wall anatomy or morphological characters of asci, ascospores, and conidia, and sporodochia in culture. The strain differs in having shorter phialides, more divergently branched phialides, and longer basal branches of the sporodochial conidiophores (Fig. 26 f).