An overview of the taxonomy, phylogeny, and typification of nectriaceous fungi in 

Cosmospora, Acremonium, Fusarium, Stilbella, and Volutella

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Abstract: A comprehensive phylogenetic reassessment of the ascomycete genus Cosmospora (Hypocreales, Nectriaceae) is undertaken using fresh isolates and historical strains, sequences of two protein encoding genes, the second largest subunit of RNA polymerase II (rpb2), and a new phylogenetic marker, the larger subunit of ATP citrate lyase (acl1). The result is an extensive revision of taxonomic concepts, typification, and nomenclatural details of many anamorph- and teleomorph-typified genera of the Nectriaceae, most notably Cosmospora and Fusarium. The combined phylogenetic analysis shows that the present concept of Fusarium is not monophyletic and that the genus divides into two large groups, one basal in the family, the other terminal, separated by a large group of species classified in genera such as Calonectria, Neonectria, and Volutella. All accepted genera received high statistical support in the phylogenetic analyses. Preliminary polythetic morphological descriptions are presented for each genus, providing details of perithecia, micro- and or macro-conidial synanamorphs, cultural characters, and ecological traits. Eight species are included in our restricted concept of Cosmospora, two of which have previously documented teleomorphs and all of which have Acremonium-like microconidial anamorphs. A key is provided to the three anamorphic species recognised in Atractrium, which is removed from synonymy with Fusarium and epitypified for two macroconidial synnematous species and one sporodochial species associated with waterlogged wood. Dialonectria is recognised as distinct from Cosmospora and two species with teleomorph, macroconidia and microconidia are accepted, including the new species D. uvellolea. Seven species, one with a known teleomorph, are classified in Fusicolla, formerly considered a synonym of Fusarium including members of the F. aquaeductuum and F. menisporoides species complex, with several former varieties raised to species rank. Originally a section of Neocentri, Macronia is raised to generic rank for five species, all producing a teleomorph and macroconidial anamorph. A new species of the Verticillium-like anamorphic genus Mariannaea is described as M. samuelii. Microconia is recognised as distinct from Fusarium and a key is included for four macroconidial species, that are usually parasites of scale insects, two of them with teleomorphs. The four accepted species of Stylenectria each produce a teleomorph and macro- and microconidial synanamorphs. The Volutella species sampled fall into three clades. Pseudonectia is accepted for a perithelial and sporodochial species that occurs on Buux. Volutella s. str. also includes perithelial and/or sporodochial species and is revised to include a synnematous species formerly included in Stilbella. The third Volutella-like clade remains unnamed. All fungi in this paper are named using a single name system that gives priority to the oldest generic names and species epithets, irrespective of whether they are originally based on anamorph or teleomorph structures. The rationale behind this is discussed.

Key words: Article 59, Buux, codon model, holomorph concept, unitary nomenclature, synnematous hyphomycetes. Taxonomic novelties: New genus: Macronia (Wollenw.) Gräfenhan, Seifert & Schroors. New species: Dialonectria uvellolea Seifert & Gräfenhan, Fusicolla violaceae Gräfenhan & Seifert, Mariannaea samuelii Seifert & Bissett, Microconra rubra Gräfenhan & Seifert. New combinations: Atractrium holubvaeae (Seifert, S.J. Stanley & K.D. Hyde) Seifert. Atractrium crassum (Wollenw.) Seifert & Schroors, Cosmospora anii (W. Gams) Gräfenhan & Schroors, Cosmospora berkleyaevana (P. Kans.) Gräfenhan, Seifert & Schroors, Cosmospora cymosa (W. Gams) Gräfenhan & Seifert, Cosmospora khandalensis (Thrum. & Sukapure) Gräfenhan & Seifert, Cosmospora lavitkiae (Zhdanova) Gräfenhan & Seifert, Cosmospora viridescens (C. Booth) Gräfenhan & Seifert, Fusicolla acetifera (Tubaki, C. Booth & T. Harada) Gräfenhan & Seifert, Fusicolla aquaeductum (Radl. & Raben.) Gräfenhan, Seifert & Schroors, Fusicolla epistroma (Höh.) Gräfenhan & Seifert, Fusicolla matroui (Hosoy & Tubaki) Gräfenhan & Seifert, Fusicolla merismoides (Corda) Gräfenhan, Seifert & Schroors, Macroconia cupularis (J. Luo & W.Y. Zhuang) Gräfenhan & Seifert, Macroconia gigas (J. Luo & W.Y. Zhuang) Gräfenhan & Seifert, Macroconia leptotheca (Niesl.) Gräfenhan & Schroors, Macroconia papilionacearum (Seaver) Gräfenhan & Seifert, Macroconia sphareia (Fückel) Gräfenhan & Schroors, Microconra dipola (Berk. & M.A. Curtis) Gräfenhan & Seifert, Microconria larvarum (Fückel) Gräfenhan, Seifert & Schroors, Pseudonectria buxi (DC.) Seifert, Gräfenhan & Schroors, Stilbella cupularis (Grev.) Gräfenhan, Stylenectria wegelianiana (Rehm) Gräfenhan, Voglmayr & Jaklitsch, Volutella citrinella (Ellis & Everh.) Seifert, Volutella consors (Ellis & Everh.) Seifert, Gräfenhan & Schroors. New name: Stylenectria carpini Gräfenhan.

INTRODUCTION

This paper focuses on phylogenetic and taxonomic reassessment of the prevailing concept of the ascomycete genus Cosmospora (Nectriaceae, Hypocreales) (Samuels et al. 1991, Rossman et al. 1999). This genus has been assumed to be polyphylectic because of its anamorphic and biological diversity, a fact recently reinforced by phylogenetic studies on a limited sampling of species (Zhang & Zhuang 2006, Luo & Zhuang 2008, Samuels 2009). The majority of described Cosmospora species have Acremonium-like or Fusarium-like anamorphs, but hypomycolycous anamorphs classified in Chaetopsis, Cylindrocladiella, Giociliodiopsis, Mariannaea, Penicillifer, Stilbella, Verticillium, and Volutella have also been associated with the genus (Samuels et al. 1991 as Nectria subgenus Dialonectria, Rossman et al. 1999). The prevailing concept of Cosmospora is unified by the teleomorph, which tends to be relatively nondescript, with usually solitary, astromatic, smooth, thin-walled perithecia, often orange or reddish, and changing to dark red in KOH, and 1-septate ascospores in a cylindrical ascus with a simple apex of refractive apical ring; for convenience we will refer to this concept as Cosmospora sensu Rossman.

Before DNA-based phylogenetic studies significantly influenced fungal taxonomy, anamorph taxonomy in the Hypocreales had shifted away from classical form-taxa towards a practice that correlated teleomorphistic and anamorphic generic concepts (Samuels
& Seifert 1987). Preceding the segregation of *Nectria sensu* Booth into many teleomorph genera in three families, Rossman (1993) suggested the delimitation of each teleomorph genus with one anamorph genus, the so-called 1:1 genus concept. Taxonomic equivalency between linked teleomorph and anamorph genera was proposed for several groups of the *Bio nicectiae*, *Nectriaceae*, and *Hypocreaceae*. Within the *Cosmospora* complex, for example, this rationale was used in the corresponding generic concepts for *Nectriciadiella* (teleomorph), with *Cylindrociadiella* (anamorph) (Schoch et al. 2000), and *Chaetopsis* *nectria* (teleomorph) with *Chaetopsis* *ina* (anamorph) (Luo & Zhuang 2010).

Booth's broad concept of *Nectria* dominated for 30 years; he recognised "groups" of species including the Epiphaea group (Booth 1959). This group, with additional species, was revised first as *Nectria* subgenus Dialonecia by Samuels et al. (1991), and then elevated to generic rank as *Cosmospora* (Rossman et al. 1999). The latter is typified by *C. coccinea* (= *Nectria coccinea*, which is a different fungus), which Saccardo (1983) listed as the only member of *Nectria* subgenus *Cosmospora*. *Cosmospora* *coccinea* produces orange, solitary, superficial perithecia and verrucose, brownish ascospores; its anamorph is *Verticillium olivaceum* (Gams 1971).

The relationship of the prevailing concept of *Cosmospora* with the generic concept of the economically important anamorph genus *Fusarium* is significant. In the present taxonomic system, about 20 *Fusarium* species or varieties are linked to *Cosmospora* sensu Rossman (Gräfenhan et al. 2008). There has been a reluctance to apply the 1:1 genus concept or strict monophyly to the present generic concept of *Fusarium*, which exhibits a striking lack of correlation with teleomorph/holomorph generic concepts in the *Nectriaceae*. Species with teleomorphs classified in other orders of ascomycetes were excluded from *Fusarium* some time ago, namely *Microdochium nivale* (Xylariaceae, Samuels & Hallett 1983) and *Plectosporium tabacinum* (Glomerellales, Palm et al. 1995). As now delimited, *Fusarium* is still linked to six teleomorph genera in the *Nectriaceae*, i.e. *Albonectria*, *Cosmospora*, *Cyanonectria*, *Gibberella* (the teleomorph genus associated with the type species of *Fusarium*), and *Haemanectria*, with some species remaining in *Nectria* sensu Booth. Members of a seventh genus, *Neocosmospora*, fall into the *Fusarium* *solani/haemanectria* clade (O'Donnell et al. 2008), but *Fusarium*-like macroconidia are produced by these species.

Throughout the modern history of *Fusarium*, taxonomists have consistently recognised the distinctiveness of several groups of species first considered as discrete taxonomic sections by Wollenweber (1931). Most species of sections *Eupionnotes*, *Macroconia*, *Pseudomicrocera*, and *Archonites* produce characteristic colonies in vitro, growing slower and producing less aerial mycelium than species of other sections (Gerlach & Nirenberg 1982), often with spreading orange, macroconidial slime known as pionnotes. As shown for most taxonomic sections of *Fusarium*, sections *Eupionnotes* and *Macroconia* are polyphyletic (O'Donnell 1993, Torzilli et al. 2002, Schroers et al. 2009). Some of the morphological characters used to define these sections, including macroconidial shape and colony characters in vitro, are plesiomorphic and shared by distantly related species. For *Acremonium*-like anamorphs, a similar or even more complex pattern of plesiomorphy is known; preliminary revisions to that generic concept are presented by Summerbell et al. (2011).

Although there have been discussions of narrowing the generic concept of *Fusarium* at specialist symposia, arguments have not been presented in print nor have nomenclatural changes been proposed. The prevailing concept of *Fusarium* is essentially that of Wollenweber (1931) and Wollenweber & Reinking (1935) with the exclusion of some species; for convenience we refer to this concept as *Fusarium sensu* Wollenweber. The need to reevaluate more than 20 anamorph generic names considered synonyms of *Fusarium* has caused some hesitancy in modifying this concept; these type studies are initiated here. Previous studies provided inconclusive phylogenetic evidence to demonstrate the distinctiveness of the *Gibberella* and *Cosmospora* clades, but sampled inadequately from other anamorph and teleomorph genera in the *Nectriaceae* (O'Donnell 1993, Zhang & Zhuang 2006, Luo & Zhuang 2008, Samuels et al. 2009). We sampled more broadly here, including 93 species originally assigned to about 11 teleomorph and 13 anamorph genera.

Our phylogenetic analysis, combined with morphological and ecological considerations, suggests the recognition of about 13 well supported lineages within *Cosmospora sensu* Rossman that can be recognised at the generic level. *Fusarium sensu* Wollenweber splits into two major groups, which we will refer to as the "terminal *Fusarium* clade" centred on *Gibberella*, and a collection of lineages in the basal part of the *Nectriaceae* that we will refer to as the "basal *Fusarium*-like clades". In the latter, we resurrect the genera *Dialonecia*, *Fusicola*, *Microcera*, and *Stylonectria* for species and varieties of the former *Fusarium* sections *Archonites*, *Eupionnotes*, *Macroconia*, *Pseudomicrocera*, and *Submicrocera*, *Acremonium* section *Nectroidea*, and several fungicolous, entomogenous, and soil-borne species classified in *Cosmospora sensu* Rossman. *Cosmospora* *s. str.* is redefined as a morphologically and phylogenetically restricted genus including only species with anamorphs originally ascribed to *Acremonium* or *Verticillium*. We raise *Nectria* sect. *Macroconia* to generic rank for a small group of species with large *Fusarium*-like macroconidia and minute perithecia. We epitypify the classical hyphomycete genus *Atractium*, sometimes listed as a synonym of *Fusarium*, and consider two other anamorph genera associated with *Cosmospora*, namely *Mariannaea* and *Volutella*.

The result is a revision of the *Cosmospora sensu* Rossman clade into segregate genera that should provide phylogenetic clarity to subsequent monographic revisions and facilitate the description of new species in appropriate genera. The basal *Fusarium*-like clades, for the most part the slow growing pionnotal species formerly associated with *Cosmospora sensu* Rossman, are distributed in seven monophyletic genera, six of them provided with pre-existing generic names. Another paper concerns genera of the terminal *Fusarium* clade, including the former *Nectria desmazeria*, with teleomorphs that morphologically are somewhat *Cosmospora*-like (Schroers et al. 2011).

In common with the papers by Schroers et al. (2011) and Summerbell et al. (2011), we adopt a single-name nomenclature, employing the oldest available generic name in combination with the oldest available species epithet, irrespective of whether these names could be interpreted as teleomorphic or anamorphic. In some cases these cross-morph combinations violate Article 59. In our opinion, the International Code of Botanical Nomenclature (ICBN, McNeill et al. 2006) should be like any legal code and be governed by its own basic principles. This is analogous to a constitution; when laws within a legal structure are found to be unconstitutional, they are rejected. Art. 59 violates Principle III of the ICBN, that the correct name is based on priority of publication. We give precedence to the Principles rather than the contradictory article and essentially reject Art. 59 as unconstitutional. According to Art. 59, when a valid and legitimate name is transferred into a genus
that does not match its karyological type, *i.e.* an anamorph epithet is moved into a teleomorph genus or visa versa, the name can be considered superfluous or incorrect or contrary to Art. 59.1, but the resulting binomial is still valid and legitimate. By this interpretation, combination of a valid, legitimate anamorph-typified epithet to a teleomorph-typified generic name or a valid teleomorph-typified epithet to an anamorph-typified generic name, results in a binomial that is incorrect for the holomorph. Incorrect names may become correct later (cf. Art. 52.3) provided they have a valid/legitimate basionym and the part of the Code (i.e. Art. 59) that makes the names incorrect is changed. According to the title of Chapter VI of the Code, Art. 59 only applies to pleomorphic fungi, *i.e.* species where both the teleomorph and anamorph(s) are known. In this interpretation, names for monomorphic species resulting from the transfer of anamorph epithets into teleomorph-typified genera or visa versa would be correct, valid, and legitimate. In this paper, we explicitly state which names may be "incorrect" according to this interpretation of the present Code. However, we hope that the growing support for single name nomenclature that was evident at the International Mycological Congresses in 2002, 2006, and 2010 will discourage anyone from attempting to "correct" them.

**MATERIALS AND METHODS**

**Fungal isolates and herbarium specimens**

Ninety-three taxa of *Nectriaceae* were included in the phylogenetic study with *Acremonium lichenicola* selected as outgroup (Table 1) based on prior analyses (Gräfenhan et al. 2008). Morphological observations of colonies and anamorph characters are based on strains grown on potato-dextrose agar (PDA; Difco), cornmeal agar (CMA; Acumedia, Lansing, Michigan) and synthetic low nutrient agar (SNA; Nirenberg 1976) in the laboratory at room temperature (about 22–25 °C) under ambient light conditions. Measurements for some structures are presented as a range of extreme observed values given in parentheses, and the number one standard deviation above and below the calculated mean, with observations of colonies and anamorph characters are based on prior analyses (Gräfenhan 2002, 2006). Morphological observations of colonies and anamorph characters are based on strains grown on potato-dextrose agar (PDA; Difco), cornmeal agar (CMA; Acumedia, Lansing, Michigan) and synthetic low nutrient agar (SNA; Nirenberg 1976) in the laboratory at room temperature (about 22–25 °C) under ambient light conditions. Measurements for some structures are presented as a range of standard deviation above and below the calculated mean, with extreme observed values given in parentheses, and the number of measured structures noted. Colour codes refer to Körnerup & Wanscher (1978). Herbarium abbreviations are from Holmgren et al. (1990). Abbreviations of culture collections follow the World Federation of Culture Collections code (wdcm.nig.ac.jp/wfcc).

**DNA extractions, PCR and DNA sequencing**

DNA extractions were performed using UltraClean Microbial DNA Isolation Kits (MO BIO Laboratories Inc., Carlsbad, California) from mycelium scraped from colonies grown on PDA using a sterile scalpel. DNA concentration and quality were determined by Nanodrop ND-1000 spectrometer (Thermo Scientific, Wilmington, Delaware) and preparations were diluted to 1–5 ng/µL of DNA template.

The second largest subunit of the RNA polymerase II (*rp2*) was amplified following the protocol of de Cock & Lévesque (2004) using the primer combinations 5F2/7cR and 7cF/11aR (O’Donnell et al. 2007) in a total reaction volume of 20 µL following the same protocol. PCR reactions were placed in an Eppendorf thermal cycler (Westbury, New York) and processed with the following temperature profile for the *rp2* regions: 3 min at 95 °C (initial denaturation), 5 cycles 45 s at 95 °C (denaturation), 45 s at 60 °C (annealing), 2 min at 72 °C (extension), followed by 5 cycles with annealing at 58 °C, followed by 30 cycles with annealing at 54 °C, with a final extension 8 min at 72 °C. The temperature profile for the *act1* region was as follows: 3 min at 95 °C, 5 cycles 45 s at 95 °C, 45 s at 64 °C, 2 min at 72 °C, followed by 5 cycles with annealing at 62 °C, followed by 30 cycles with annealing at 56 °C, with a final extension 8 min at 72 °C. For forward and reverse strands, sequencing reactions were performed directly without cleaning PCR amplicons, using a BigDye sequencing kit (Applied Biosystems, Foster City, California) on an ABI3130 DNA Analyzer (Applied Biosystems). The following profile was used for the sequencing reactions: 95 °C for 3 min, then for 40 cycles at 95 °C for 30 s, 50 °C for 15 s for 15 s, 60 °C for 2 min. Contig sequences were assembled using Sequencer v. 4.9 (Gene Codes Corporation, Ann Arbor, Michigan) and aligned manually using BioEdit 7 (Hall 1999). Protein coding DNA sequences were aligned along the reading frame of the corresponding amino acid sequence and divided into 3 partitions, *rp2* region 5–7, *rp2* region 7–11, and *act1*. Intergenic spacer regions and introns of the *rp2* and *act1* gene sequences could not be reliably aligned and were excluded from the final alignment. Additional ITS sequences were generated for some of the species mentioned below using the methods described by Nguyen & Seifert (2008).

All DNA sequences generated in this study are deposited in GenBank (accession numbers listed in Table 1 and in the Taxonomy part as barcodes). We have designated some of these as "DNA barcodes" when they represent type, authentic, or thoroughly validated strains.

**Phylogenetic analyses**

The combined and partitioned data set of the protein encoding regions of *rp2* and *act1* was used to search for the best maximum likelihood (ML) tree employing the GARLI v. 1 software (Zwickl 2006) implemented by the CIPRES project at the San Diego Supercomputer Center (www.phylo.org). The best-fit substitution model under the Akaike information criterion (Akaike 1974) was determined by using Modeltest v. 3.7 (Posada & Crandall 1998) and PAUP v. 4.0b10 (Swofford 2003). The GTR + I + G nucleotide substitution model was selected, which assumes an estimated proportion of invariant sites and 8 gamma-distributed rate categories to account for rate heterogeneity across sites. 100 independent ML heuristic phylogenetic analyses were performed using a starting tree generated by stepwise-addition (attachmentspertonax = 2) and 10 000 generations without topology improvement parameter. To correct for positive and divergent selection in molecular evolution of protein encoding DNA sequences, ML analyses were performed with GARLI using a codon substitution model that considers the ratio of nonsynonymous (dN) to synonymous (dS) rates of nucleotide substitution (dN/dS = ω). The GTR-like substitution model was selected with F3+4 codon frequencies (observed frequency at each codon position) and dN/dS values and proportions falling in three discrete categories ω1 < ω2 < ω3 (M3 model with site classes K = 3, Yang et al. 2000). Ten independent ML heuristic phylogenetic analyses were performed using a starting tree generated by stepwise-addition (attachmentspertonax = 2) and 10 000 generations without improving the topology parameter.
| Unitary names used in phylogenies | Teleomorph name (most recent) | Collector Depositor | Country | Strain | GenBank Accession No. | rpb2 | acl1 | ITS | "TSU" | rps16 | No. † | Collector Depositor | Country | Substratum | GenBank Accession No. | Other No. † | Taxa used in molecular phylogenetic analysis. |
|----------------------------------|-------------------------------|---------------------|---------|--------|----------------------|------|-----|-----|-------|-------|--------|---------------------|---------|-----------|---------------------|------------|------------------------------------------|
| Acremonium lichenicola W. Gams | Acremonium lichenicola W. Gams | CBS 425.66* K.W. Gams | Germany | Betula sp. old leaf | HQ897742 | - | - | - | - | - | - | - | - | - | - |
| Acremonium macroclavatum Ts. Watan. | Acremonium macroclavatum Ts. Watan. | CBS 786.69* J.E. Bier | Japan | Bank of woody stem | HQ897736 | - | - | - | - | - | - | - | - | - | - |
| Acremonium tsugae W. Gams | Acremonium tsugae W. Gams | CBS 788.69* J.E. Bier | Canada | Bank of woody stem | HQ897738 | - | - | - | - | - | - | - | - | - | - |
| "Albonectria" albida (Rossman) Guu & Y.M. Ju | "Albonectria" albida (Rossman) Guu & Y.M. Ju | BBA 67603* ATCC 44544; C.T.R. 71-110 | Jamaica | Decaying fungoid body | HQ897769 | - | - | - | - | - | - | - | - | - | - |
| Albonectria albosuccinea (Pat.) Rossman & Samuels | Albonectria albosuccinea (Pat.) Rossman & Samuels | BBA 64502* ATCC 44544; C.T.R. 71-110 | Canada | Decaying fungoid body | HQ897769 | - | - | - | - | - | - | - | - | - | - |
| Albonectria rigidiuscula (Berk. & Broome) Rossman & Samuels | Albonectria rigidiuscula (Berk. & Broome) Rossman & Samuels | CBS 102163 ATCC 208923; BBA 64786; G.J.S. 84-426 | New Zealand | Decaying fungoid body | HQ897769 | - | - | - | - | - | - | - | - | - | - |
| "Albonectria" verrucosa (Pat.) Rossman & Samuels | "Albonectria" verrucosa (Pat.) Rossman & Samuels | CBS 102163 ATCC 208923; BBA 64786; G.J.S. 84-426 | New Zealand | Decaying fungoid body | HQ897769 | - | - | - | - | - | - | - | - | - | - |
| Atractium crassum (Wollenw.) Seifert & Gräfenhan | Atractium crassum (Wollenw.) Seifert & Gräfenhan | CBS 180.31* NRRL 20894 H.W. Wollenweber | Germany | Water tap | HQ897778 | - | - | - | - | - | - | - | - | - | - |
| Atractium stilbaster Link | Stilbella fusca (Sacc.) Seifert | DAOM 215627 K.A. Seifert | Canada / Quebec | Decaying fungoid body | HQ897778 | - | - | - | - | - | - | - | - | - | - |
| Fuscari decemcellulare Brick | Fuscari decemcellulare Brick | CBS 122570 BPI 863840; G.J.S. 01-170 | Cameroon | Decaying fungoid body | HQ897778 | - | - | - | - | - | - | - | - | - | - |
| Cosmospora arxii (W. Gams) Gräfenhan & Schroers | Acremonium arxii W. Gams | CBS 180.31* NRRL 20894 H.W. Wollenweber | Germany | Water tap | HQ897778 | - | - | - | - | - | - | - | - | - | - |
| Cosmospora butyri (J.F.H. Beyma) Gräfenhan, Seifert & Schroers | Tilachlidium butyri J.F.H. Beyma | CBS 180.31* NRRL 20894 H.W. Wollenweber | Germany | Water tap | HQ897778 | - | - | - | - | - | - | - | - | - | - |
| Cosmospora coccinea Rabenh. | Cosmospora coccinea Rabenh. | CBS 301.38* MUCL 9950 K.W. Gams | Denmark | Decaying fungoid body | HQ897778 | - | - | - | - | - | - | - | - | - | - |
| Cosmospora cymosa (W. Gams) Gräfenhan & Seifert | Acremonium cymosum W. Gams | CBS 301.38* MUCL 9950 K.W. Gams | Denmark | Decaying fungoid body | HQ897778 | - | - | - | - | - | - | - | - | - | - |
| Cosmospora cf. viridescens (C. Booth) Gräfenhan & Seifert | Nectria cf. viridescens C. Booth | CBS 102433 M. Reblova | Czech Republic | Decaying fungoid body | HQ897778 | - | - | - | - | - | - | - | - | - | - |
| Cosmospora khandalensis (Thirum. & Sukapure) Gräfenhan & Seifert | Cephalosporium khandalense Thirum. & Sukapure | CBS 122305* A.R. 4385; BPI 878274 | India | Decaying fungoid body | HQ897778 | - | - | - | - | - | - | - | - | - | - |
| Cosmospora lavitskiae (Zhdanova) Gräfenhan & Seifert | Gliomastix lavitskiae Zhdanova | CBS 530.68* ATCC 18666; IMI 133984 | Ukraine | Decaying fungoid body | HQ897778 | - | - | - | - | - | - | - | - | - | - |
| Cosmospora stegonsporii Rossman, D.F. Farr & Akulov | Cosmospora stegonsporii Rossman, D.F. Farr & Akulov | CBS 122305* A.R. 4385; BPI 878274 | India | Decaying fungoid body | HQ897778 | - | - | - | - | - | - | - | - | - | - |
| Cosmospora cf. viridescens (C. Booth) Gräfenhan & Seifert | Nectria cf. viridescens C. Booth | CBS 102433 M. Reblova | Czech Republic | Decaying fungoid body | HQ897778 | - | - | - | - | - | - | - | - | - | - |
| Collector/Depositor | Country | Substratum | GenBank Accession No. † | Other No. † | Unitary names used in phylogenies | Anamorph name (most recent) | Strain † | Other No. † | Collector name (most recent) |
|---------------------|---------|------------|-------------------------|-------------|----------------------------------|-----------------------------|----------|-------------|-----------------------------|
| Collector/Depositor | Country | Substratum | GenBank Accession No. † | Other No. † | Unitary names used in phylogenies | Anamorph name (most recent) | Strain † | Other No. † | Collector name (most recent) |
| Collector/Depositor | Country | Substratum | GenBank Accession No. † | Other No. † | Unitary names used in phylogenies | Anamorph name (most recent) | Strain † | Other No. † | Collector name (most recent) |
| Collector/Depositor | Country | Substratum | GenBank Accession No. † | Other No. † | Unitary names used in phylogenies | Anamorph name (most recent) | Strain † | Other No. † | Collector name (most recent) |
| Collector/Depositor | Country | Substratum | GenBank Accession No. † | Other No. † | Unitary names used in phylogenies | Anamorph name (most recent) | Strain † | Other No. † | Collector name (most recent) |
| Collector/Depositor | Country | Substratum | GenBank Accession No. † | Other No. † | Unitary names used in phylogenies | Anamorph name (most recent) | Strain † | Other No. † | Collector name (most recent) |

Table 1. Continued.
| Unitary names used in phylogenies | Teleomorph name (most recent) | Anamorph name (most recent) | Strain † | Other No. † | Collector/Depositor | Country | Substratum | GenBank Accession No. ‡ | rpb2 | acl1 | ITS | LSU |
|---------------------------------|-----------------------------|-----------------------------|----------|-------------|---------------------|---------|------------|------------------------|------|------|-----|-----|
| **Fusarium sambucinum** Fuckel | Gibberella pulicaris (Fr.) Saoc. | *Fusarium sambucinum* FUCKEL | BBA 7096 | H.I. Nirenberg | Germany | Humulus lupulus | HQ997751 | HQ997827 | – | – | – | – |
| **Fusarium sublunatum** Reinking | Gibberella moniliformis (Sacc.) Wineland | *Fusarium sublunatum* Reinking | BBA 62431 | O.A. Reinking | Costa Rica | Soil of banana plantation | HQ997780 | HQ997916 | HQ997830 | – | – | – | – |
| **Fusarium verticillioides** (Sacc.) Nirenberg | Gibberella moniliformis (Sacc.) Wineland | *Fusarium verticillioides* (Sacc.) Nirenberg | NRRL 20396 | FSCG 7600; FRC M-3125 | USA / California | Zea mays | FVEG01986 | FVEG01987 | – | – | – | – |
| **Fusarium sambucinum** Fuckel | Fusarium sambucinum Fuckel | BBA 62195; CBS 119875; K.A.S. 2872; MRC 1652 | | | Germany | Solanum lycopersicum | HQ997698 | HQ997836 | HQ997877 | – | – | – | – |
| **Fusarium sublunatum** Reinking | Fusarium sublunatum Reinking | BBA 62431* | CBS 189.34; NRRL 13384; NRRL 20840 | H.I. Nirenberg | Germany | Humulus lupulus | HQ997751 | HQ997827 | – | – | – | – |
| **Fusarium verticillioides** (Sacc.) Nirenberg | Fusarium verticillioides (Sacc.) Nirenberg | DAOM 238648 | IMI 181488; NRRL 20827 | R. Schneider | Germany | Solanum lycopersicum | HQ997698 | HQ997836 | HQ997877 | – | – | – | – |
| **Fusarium sambucinum** Fuckel | Fusarium sambucinum Fuckel | BBA 62195; CBS 119875; K.A.S. 2872; MRC 1652 | | | Germany | Solanum lycopersicum | HQ997698 | HQ997836 | HQ997877 | – | – | – | – |
| **Fusarium sublunatum** Reinking | Fusarium sublunatum Reinking | BBA 62431* | CBS 189.34; NRRL 13384; NRRL 20840 | H.I. Nirenberg | Germany | Solanum lycopersicum | HQ997698 | HQ997836 | HQ997877 | – | – | – | – |
| **Fusarium verticillioides** (Sacc.) Nirenberg | Fusarium verticillioides (Sacc.) Nirenberg | DAOM 238648 | IMI 181488; NRRL 20827 | R. Schneider | Germany | Solanum lycopersicum | HQ997698 | HQ997836 | HQ997877 | – | – | – | – |
| **Fusarium sambucinum** Fuckel | Fusarium sambucinum Fuckel | BBA 62195; CBS 119875; K.A.S. 2872; MRC 1652 | | | Germany | Solanum lycopersicum | HQ997698 | HQ997836 | HQ997877 | – | – | – | – |
| **Fusarium sublunatum** Reinking | Fusarium sublunatum Reinking | BBA 62431* | CBS 189.34; NRRL 13384; NRRL 20840 | H.I. Nirenberg | Germany | Solanum lycopersicum | HQ997698 | HQ997836 | HQ997877 | – | – | – | – |
| **Fusarium verticillioides** (Sacc.) Nirenberg | Fusarium verticillioides (Sacc.) Nirenberg | DAOM 238648 | IMI 181488; NRRL 20827 | R. Schneider | Germany | Solanum lycopersicum | HQ997698 | HQ997836 | HQ997877 | – | – | – | – |
| Teleomorph name | Strain | Collector/ Depositor | Country | Substratum | GenBank Accession No. |
|-----------------|--------|----------------------|---------|------------|---------------------|
| *Heliscus lugdunensis* Sacc. & Therry | CBS 125485 | T. Gräfenhan | USA / Arizona | Populus fremontii, twigs in stream | HQ897731, HQ897867 |
| *Heliscus submersus* H.J. Hud. | CBS 394.62* | H.J. Hudson | UK | – | HQ897707, HQ897845, HQ897796 |
| *Cosmospora leptothesphaerarum* (Nielssen) Grafenhan & Schroers | CBS 10001 | L. Rommelaars | Netherlands | On Leptosphaeria on dead stem of Urtica dioica | HQ897755, HQ897981, HQ897810 |
| *Macroconia papilionacearum* (Seaver) Grafenhan & Safert | CBS 125495 | T. Gräfenhan | USA / Florida | Black ascomycete on Fabaceae | HQ897776, HQ897912, HQ897826 |
| *Macroconia sp.* | CBS 125496 | T. Gräfenhan | USA / Arizona | – | HQ897732, HQ897868 |
| *Mariannaea elegans* (Corda) Samson | DAOM 236709 | K.A. Seifert | Canada / Ontario | Betula sp., wood | HQ897747, HQ897888, HQ894376 |
| *Mariannaea samuelsei* Seifert & Bisetti | DAOM 235814* | J. Bissett | Guatemala | Soil under Podocarpus | HQ897752, HQ897888, HQ894376 |
| *Microcera coccophila* Deam. | CBS 310.34 | H.W. Wollenweber | Italy | Scale insect on Laurus nobilis | HQ897705, HQ897843, HQ897794 |
| *Microcera dipla* (Berk. & M.A. Curtis) Grafenhan & Seifert | CBS 125496 | T. Gräfenhan | USA / Arizona | Quercus sp., branch in stream of water | HQ897732, HQ897868 |
| *Microcera larvarum* (Fuckel) Grafenhan, Seifert & Schroers | CBS 169.30 | H.W. Wollenweber | Japan | Aphids on Pyrus communis | HQ897717, HQ897855 |
| *Microcera rubra* Grafenhan & Seifert | CBS 638.76; NRRL 20475; NRRL 22102 | W. Gerlach | Iran | Quadraspidiotus perniciosus on living on branch of Prunus domestica | HQ897763, HQ897899, HQ897817 |
| *Nalanthamala diospyri* (Crand.) Schneers & J.M. Wingfield | CBS 125499 | T. Gräfenhan | USA / Arizona | On fungus on decorticated wood | HQ897702, HQ897907, HQ897791 |
| *Nectria cinereopapillata* Henn. & E. Nyman | CBS 264.36 | H.W. Wollenweber | Sierra Leone | Cassia siliquosa | HQ897710, HQ897848, HQ897799 |
| *Nectria* cf. flavoviridis (Fuckel) Wollenw. | CBS 380.50* | W. Gerlach | Iran | Quadraspidiotus perniciosus on living on branch of Prunus domestica | HQ897763, HQ897899, HQ897817 |
| *Nectria magnoliae* M.L. Lohman & Hepting | CBS 380.50* | W. Gerlach | Iran | Quadraspidiotus perniciosus on living on branch of Prunus domestica | HQ897763, HQ897899, HQ897817 |
| *Nectria nigrescens* Cooke | CBS 125000 | T. Gräfenhan | Canada / Ontario | Acer sp., twig | HQ897757, HQ897893, HQ897812 |
| *Nectria pseudotrichica* Berk. & M.A. Curtis | DAOM 235820 | T. Gräfenhan | USA / Florida | Dead herbaceous plant | HQ897706, HQ897844, HQ897795 |

**Table 1.**
Table 1. (Continued).

| Unitary names used in phylogenies | Teleomorph name | Anamorphic (most recent) | Collector | Deposter | Other No. | Strain | GenBank Accession No. | ITS | LSU |
|----------------------------------|----------------|--------------------------|----------|----------|----------|-------|-----------------------|-----|-----|
| "Nectria" rishbethii | Anamorph | Cosmospora rishbethii | C. Booth | Cosmospora rishbethii | CBS 496.67 | IMI 070248b | HQ897714 | H0897716 | L3613 |
| "Nectria" rubropeziza | Anamorph | Cosmospora rubropeziza | Wollenw. | Nectria rubropeziza | CBS 234.31 | H.W. Wollenweber | HQ897761 | H0897765 | – |
| "Nectria" setofusariae | Anamorph | Nectria setofusariae | Samuels & Nirenberg | Nectria setofusariae | CBS 125489 | H.A. 1995 | HQ897711 | H0897765 | L3613 |
| "Nectria" ventricosa | Anamorph | Cosmospora ventricosa | C. Booth | Nectria ventricosa | CBS 745.79 | H.W. Wollenweber | HQ897761 | H0897765 | L3613 |
| "Nectria" sp. CBS 125491 | Anamorph | Stylonectria sp. | T.G. 2007-34 | – | T. Gräfenhan | – | – | – | – |
| "Nectria" sp. CBS 125492 | Anamorph | Thelonectria sp. | T.G. 2007-21 | – | T. Gräfenhan | – | – | – | – |

Note: The table continues with similar entries, each representing different species and their teleomorph and anamorph names, collectors, depositories, and GenBank accession numbers.
Non-parametric bootstrapping of 1 000 ML pseudoreplicates of the data was used to assess clade support with GARLI. Because of the extended time necessary for ML bootstrap analysis under the M3 codon model, the measure of clade support was calculated using the parameters of the GTR + I + G nucleotide model given above. ML bootstrap probabilities (ML-BP) for the splits were mapped onto the best phylogenetic tree inferred under the M3 codon substitution model using SumTrees of the DendroPy v. 3.7 phylogenetic computing library (Sukumaran & Holder 2010).

Bayesian posterior probabilities (PP) were obtained from the combined and partitioned rpb2/acl1 data set using MrBayes v. 3.1.2 (Ronquist & Huelsenbeck 2003) implemented by the CIPRES project (see above). The GTR + I + G substitution model was selected assuming an estimated proportion of invariant sites and 4 gamma-distributed rate categories to account for rate heterogeneity across sites. Two independent Markov chain Monte Carlo analysis (MCMC) runs each with 4 chains were performed simultaneously. The analysis was run for 10 000 000 generations, sampling every 1 000 generations for a total of 10 001 trees. The first 1 500 000 generations were discarded as burn-in. Each of the two independent MCMC runs yielded 8 501 trees from each partition. The resulting six tree files (total 51 006 trees) were used to calculate PPs. These posterior probabilities were mapped onto the best phylogenetic tree using SumTrees of the DendroPy package.

Heuristic searches for the most parsimonious (MP) trees using PAUP v. 4.0b10 (Swoford 2003) were based on 1 026 parsimony informative, unordered and equally weighted characters; gaps were treated as missing data. Starting trees were obtained via 100 stepwise, random addition sequences. Other settings included auto-increase for MAXTREES, the tree-bisection-reconnection branch-swapping algorithm, the MULTREES option, and assigning any possible character state to an internal node with STEPMATRIX. MP bootstrap probabilities (MP-BP) were assessed by 1 000 heuristic pseudoreplicates using the same settings as above but with 20 stepwise, random addition sequences. By using SumTrees of the DendroPy package, the MP-BP support for the splits were mapped onto the best phylogenetic tree.

**RESULTS**

**Sequence alignment**

The combined and partitioned data set of two protein encoding genes for 93 taxa and outgroup consisted of 2 250 bp, translating to 750 amino acids. The rpb2 sequences (1 764 bp) had two coding regions (rpb2 5–7 and rpb2 7–11) with an intergenic spacer, which was removed from the final alignment. The acl1 amplicon comprised a coding region of 420 bp and a single intron of 200–500 bp, which was also removed.

**Phylogenetic analyses**

One hundred independent ML analyses under the GTR + I + G nucleotide substitution model of the combined and partitioned data set (rpb2 5–7 with 488 parsimony-informative characters, rpb2 7–11 with 387 parsimony-informative characters, and
acr1 with 206 parsimony-informative characters) resulted in a single best ML tree with ∼lnL = −57.309.9782 (not shown). The parameters for the GTR + I + G model of the rpb2 5–7 partition were as follows: Estimated base frequencies; A = 0.2098, C = 0.3050, G = 0.2538, T = 0.2379; substitution rates AC = 1.234, AG = 2.844, AT = 0.638, CG = 0.933, CT = 2.489, GT = 1.000; and three estimated non-synonymous rate categories ω1 = 0.0020 with p1 = 0.6471, ω2 = 0.0276 with p2 = 0.2452, ω3 = 0.3214 with p3 = 0.1077. The parameters for the M3 codon model of the rpb2 5–7 partition were as follows: 61 empirical codon frequencies (F3×4 method); substitution rates AC = 1.234, AG = 2.380, AT = 1.222, CG = 0.743, CT = 2.758, GT = 1.000; and three estimated non-synonymous rate categories ω1 = 0.0020 with p1 = 0.8918, ω2 = 0.0925 with p2 = 0.0985, ω3 = 0.5436 with p3 = 0.0097. The parameters for the M3 codon model of the acr1 partition were as follows: 61 empirical codon frequencies (F3×4 method); substitution rates AC = 1.863, AG = 3.515, AT = 1.290, CG = 1.264, CT = 3.346, GT = 1.000; and three estimated non-synonymous rate categories ω1 = 0.0031 with p1 = 0.8025, ω2 = 0.1007 with p2 = 0.1211, ω3 = 0.4420 with p3 = 0.0763. These dN/dS ratios (ω < 1) verify a significant departure from neutrality (ω ≈ 1) of the species of the terminal group is the sister clade of Cosmospora sensu stricto and Chaetopsina, and Volutella is a well supported sister species of Volutella, confirming the close phyletogenetic relationship of Chaetopsina and Volutella (Zhang & Zhuang 2006, Luo & Zhuang 2010). Although not strongly supported, the Volutella/Chaetopsina group is the sister clade to a diverse fungal clade consisting of species of Calonectria, Cylindrocarpon, Heliscus, Mariannaea, and Neocentra. The second major clade includes species formerly classified as Nectria, and C. wegeiniana. This clade is strongly supported and comprises species having acomata with perithecial walls mainly consisting of two regions, and which are probably host-specific. These species are transferred to Stylonectria in the taxonomic section below. The third and largest clade includes several subclades including the type species of Cosmospora, C. coccinea, and species with Fusarium-, Acremonium- and Verticillium-like anamorphs, which are classified in Cosmospora sensu stricto, Diallopectoria, Fusicolla, Macroconia, and Microcera clade below. Cosmospora coccinea forms a strongly supported clade with other well-known species of the genus with Acremonium-like anamorphs, such as C. butyi, C. cymosa, and C. viride. This clade contains a group of species with similar microconidial anamorphs and a fairly constant ecological niche, delineating the new generic concept of Cosmospora s. str. Basal to Cosmospora is the strongly supported Diallopectoria clade, which contains D. episphaeria and a new species, D. ulveola. With "Nectria" rishbethii as a sister species, this subclade is delimited from another strongly supported subclade with species of Macroconia and Microcera, and Fusicolla matuoi. Macroconia and Microcera are sister clades, and include species such as Macroconia papilionacearum and Mac. leptosphaeriae as well as Microcera coccophila, Mic. diploa, and Mic. larvarum. These subclades, together with a few "residual" species classified in Fusarium such as "F." caviespermum, "F." ciliatum, "F." melanochlorum, and "F." merismoides var. chlamydomastigale, are all phylogenetically distinct from the terminal Fusarium clade discussed below. The terminal Fusarium clade contains a group of fungi with Cosmospora-like teleomorphs, of which only "Nectria" zealandica was formally combined in Cosmospora (Nirenberg & Samuels 2000). Fig. 1. (p. 89) Maximum likelihood (ML) tree under the M3 codon model inferred from combined rpb2 + acr1 gene sequence data set. Negative-log likelihood (∼lnL) of the ML tree is −54.991.4885. Branches with ML-BP and MP-BP values of > 75 % and PP scores > 0.95 are in bold. Internodes that are supported with individual values of ML-BP or MP-BP > 75 % or PP scores > 0.95, respectively, are drawn in thicker lines on the best ML tree generated for the M3 codon model. Internodes with significant clade support are drawn in thicker lines on the best ML tree topology (Fig. 1). Nodes were considered strongly supported when ML bootstrap proportions (ML-BP) is ≥ 75 %, Bayesian posterior probabilities (PP) is ≥ 0.95, and MP bootstrap proportions (MP-BP) is ≥ 75 % (Lutzoni et al. 2004). Polyphyly of Cosmospora sensu Rossman In the best ML tree (Fig. 1), species formerly placed in Cosmospora sensu Rossman fall into several major clades. The first major clade includes Volutella with four strains of three species, V. ciliata, V. citrinella ("Cosmospora" sibillumae) and V. consors ("C." consors), in a strongly supported clade. Chaetopsina penicillata (= Chaetopsinectria or "Cosmospora" chaetopsinectriae) is a well supported sister species of Volutella, confirming the close phyletogenetic relationship of Chaetopsina and Volutella (Zhang & Zhuang 2006, Luo & Zhuang 2010). Although not strongly supported, the Volutella/Chaetopsina group is the sister clade to a diverse fungal clade consisting of species of Calonectria, Cylindrocarpon, Heliscus, Mariannaea, and Neocentra. The second major clade includes species formerly classified as Nectria, and C. wegeiniana. This clade is strongly supported and comprises species having acomata with perithecial walls mainly consisting of two regions, and which are probably host-specific. These species are transferred to Stylonectria in the taxonomic section below. The third and largest clade includes several subclades including the type species of Cosmospora, C. coccinea, and species with Fusarium-, Acremonium- and Verticillium-like anamorphs, which are classified in Cosmospora sensu stricto, Diallopectoria, Fusicolla, Macroconia, and Microcera clade below. Cosmospora coccinea forms a strongly supported clade with other well-known species of the genus with Acremonium-like anamorphs, such as C. butyi, C. cymosa, and C. viride. This clade contains a group of species with similar microconidial anamorphs and a fairly constant ecological niche, delineating the new generic concept of Cosmospora s. str. Basal to Cosmospora is the strongly supported Diallopectoria clade, which contains D. episphaeria and a new species, D. ulveola. With "Nectria" rishbethii as a sister species, this subclade is delimited from another strongly supported subclade with species of Macroconia and Microcera, and Fusicolla matuoi. Macroconia and Microcera are sister clades, and include species such as Macroconia papilionacearum and Mac. leptosphaeriae as well as Microcera coccophila, Mic. diploa, and Mic. larvarum. These subclades, together with a few "residual" species classified in Fusarium such as "F." caviespermum, "F." ciliatum, "F." melanochlorum, and "F." merismoides var. chlamydomastigale, are all phylogenetically distinct from the terminal Fusarium clade discussed below. The terminal Fusarium clade contains a group of fungi with Cosmospora-like teleomorphs, of which only "Nectria" zealandica was formally combined in Cosmospora (Nirenberg & Samuels 2000).
The terminal clade includes "Nectria" desmazeri and "N." atrofusc, and is dealt with in more detail by Schroers et al. (2011).

As a singleton, "Nectria" diminuta does not group with any of the clades mentioned above. In all analyses under various substitution models (data not shown), "N." diminuta fell neither in the terminal Fusarium clade nor the basal Fusarium-like clade nor any of the Cosmospora sensu Rossman groups (Fig. 1). This positional artifact may be caused by long-branch attraction or a paucity of parsimony-informative characters for the basal taxa in the combined DNA sequence data set.

Polyphyly of Fusarium sensu Wollenweber

The genus Fusarium is taxonomically linked to the teleomorph genus Gibberella, because they share the same species as type, F. sambucinum and G. pulicaris. In nature, Gibberella teleomorphs occur less frequently than their Fusarium anamorphs (Rossman et al. 1999). In the ML tree (Fig. 1), the Gibberella clade, representing Fusarium in the strict sense and including the type species in addition to F. graminearum, F. subulatum, and F. verticillioides, is strongly supported. In Fig. 1 and Schroers et al. (2011), Gibberella is the sister clade to Cyanonectria. The terminal Fusarium clade in Fig. 1, including species with teleomorphs described in Albionectria, Cyanonectria, Gibberella, Haematonecrtia, and Neocosmospora, did not receive a statistically significant support similar to that obtained in other phylogenetic analyses (Schroers et al. 2009).

The basal lineage of the terminal Fusarium clade is represented by the "Nectria" ventricosa species complex. Within the terminal Fusarium group, members of Albionectria and the Haematonecrtia/Neocosmospora species complex as well as the species pair "Albionectria" albida and "Fusarium" nematophilum always formed strongly supported groups.

The basal Fusarium-like clade, with numerous members formerly classified in Fusarium sections Arachnites, Eupionnotes, Macroonia, Pseudomicrocera, and Submicrocera, is phylogenetically and phenotypically distinct from the terminal Fusarium clade mentioned above. The basal clade splits into several subclades similar to what is described above for Cosmospora sensu Rossman. Therefore we have given these groups genus rank in the taxonomy part below.

Another genus of Fusarium-like species is represented by Atractium. Atractium crassum ("Fusarium" merismoides var. crassum) did not fall within the basal or terminal Fusarium clades. Together with Atractium stibaster, it forms a strongly supported sister lineage to a group of fungi including species of Chaetopsisina, Pseudeonectria, and Volutella.

Polyphyly of Volutella sensu lato

As mentioned above, Volutella and Chaetopsisina form a well supported lineage that is distinct from Cosmospora s. str. and the basal Fusarium-like clade. The type of the genus Pseudeonectria, P. buxii, together with another similar species (BBA 71336), form a strongly supported sister group to the Volutella/Chaetopsisina lineage. Chaetopsisina separates Pseudeonectria from species of Volutella s. str. In contrast to the above-mentioned clades, "Pseudeonectria" pachysandricona and "Nectria" rubropezzia comprise a fairly well supported clade that branches off near the root of the tree and that separates the basal from the terminal Fusarium clade (Fig. 1). Thus, "P." pachysandricona is only distantly related to the type species of Pseudeonectria and the Volutella s. str. group.

DISCUSSION

In revising the taxa associated with Cosmospora sensu Rossman, we focused on both teleomorph and anamorph phenotypes and ecological parameters guided by molecular phylogenetics. Resolving the taxonomy and nomenclature of Cosmospora requires resolving the phylogenetic relationships of many species presently included in Fusarium sensu Wollenweber. Previously published phylogenies of Fusarium, e.g. Summerbell & Schroers (2002), O'Donnell et al. (2010), sampled sparingly from teleomorphs of the Nectriaceae associated with other anamorph genera. It is clear from the analysis presented here in Fig. 1 and elsewhere in this volume by Chaverri et al. (2011), that as presently defined, Fusarium is not monophyletic. The basal Fusarium-like lineages and terminal Fusarium clade are separated by other genera that represent large genetic and taxonomic diversity. Although the sampling of species outside of the core Fusarium clade exceeds that of previous studies, this is still a relatively small subsample of these other genera. For example, Cylindrocladium, represented by one species here, includes about 50 known species, and the Cylindrocarpus clade including the teleomorph genera Ilyonectria, Neonectria, Rugonecrtia, and Thelonecrtia, and the anamorph genus Campylocarpus (see Chaverri et al. 2011), has at least 70 species. Volutella, discussed below, is probably similarly speciose, although no comprehensive revision exists. The hyphomycete genera Cylindrocladium, Helicus, and Marianneae and many Acremonium-like species also occur in this clade.

In our analyses based on two genes including a standard barcode marker for Fusarium, rpb2, and a new phylogenetic marker, acf1, statistical support is weak for the backbone of the phylogenetic tree. Similar problems exist with published nuclear ribosomal large subunit trees, e.g. Summerbell & Schroers (2002), Zhang & Zhuang (2006), and Luo & Zhuang (2008). In the five gene analyses by Chaverri et al. (2011), the statistical support for the backbone of the Nectriaceae is stronger, and the few members sampled in the basal Fusarium-like clade and terminal Fusarium clade both form well-supported, distinct monophyletic groups. It would be preferable if the bootstrap and probability support for the relative arrangement of these clades were stronger, but in a polyphasic treatment, this is only one kind of evidence. Although molecular analyses do not strongly support our conclusion that the basal and terminal clades of Fusarium are phylogenetically distinct, there are also no data to support the taxonomic hypothesis that Fusarium sensu Wollenweber is monophyletic. Thus, neither monophyly nor the 1:1 teleomorph:anamorph genus argument supports the classical concept of Fusarium. We are confident that additional DNA sequencing data will add support to our conclusion that these major clades diverged long ago. Our decision results in a monophyletic concept of Fusarium s. str., although the terminal Fusarium clade retains some problematic groups that will require further consideration (cf. Schroers et al. 2011). Additional sampling of outlying Fusarium-like species will undoubtedly lead to the recognition of other genera.

The Hypocreales is an anamorph rich order, with the majority of holomorphic species having at least one anamorph, and with many apparently solely anamorphic species. One of the main character suites of the Nectriaceae are sporodochial anamorphs with slimy macroconidia produced from phialides, which are broadly distributed in the family and probably represent the plesiomorphic condition. The three best known macroconidial groups were placed in the classical genera Fusarium sensu Wollenweber, Cylindrocarp,
clades, in particular seem to have disappeared. Verticillate anamorphs occur in some似乎 disappeared, while in other lineages, microconidia and enveloped in slime. These are probably also plesiomorphic in synanamorphs, with small ameroconidia produced from phialides and microconidial, Fusarium tasmanicum (McAlpine) ≡ Aschersonia henningsii Koord. 1907

### Table 2. Anamorphic genera reported as synonyms of *Fusarium* and interpretation of their type species according to present knowledge.

| Generic name    | Type species                      | Synonymy proposed by                      | Identity of type species                           | Present status                      |
|-----------------|-----------------------------------|-------------------------------------------|---------------------------------------------------|-------------------------------------|
| Fusisporium Link 1809 | *F. aurantiacum* Link 1809 : Fr. | Wollenweber (1916)                                           | *F. graminum* Corda or *F. sporotrichoides* Sherb.  | = Fusarium, Gams & Nirenberg 1989  |
| Atractium Link 1809   | *A. stibaster* Link 1809         | Wollenweber & Reinking (1935)                | *A. stibaster* Link                                | Distinct genus in Nectriaceae, this paper |
| Selenosporium Corda 1837 | *S. tuberculareoides* Corda 1837  | Lindau (1910), Wollenweber & Reinking (1935) | *F. avenaceum* Corda or *F. s. l. teutoni* Nees    | = Fusarium, Holubová-Jechová et al. 1994 |
| Microcera Desm. 1848 | *M. coccophila* Desm. 1848      | Wollenweber & Reinking (1935)                | *M. coccophila* Desm.                             | Distinct genus in Nectriaceae, this paper |
| Pionnotes Fr. 1849     | *P. capillata* (Schw.) Fr. 1849   | Wollenweber & Reinking (1935)                | *Dacrymyces* sp. (PHI)                            | = Dacrymyces, Seifert et al. in prep. |
| Fusicolla Bonord. 1851 | *F. betae* (Desm. : Fr.) Bonord. 1851 | Wollenweber (1916), Wollenweber & Reinking (1935) | *Fusicolla betae* (Desm.) Bonord.                  | Distinct genus in Nectriaceae, this paper |
| Sporothricella P. Karst. 1887 | *S. rosea* P. Karst. 1887         | Wollenweber & Reinking (1935)                | *F. sporotrichoides* Sherb.                       | = Fusarium                            |
| Lachnidium Giard 1891 | *L. acridorum* Giard 1891        | Wollenweber & Reinking (1935)                | *F. solani* complex                               | = Fusarium, Henningsii 1993          |
| Discocolla P et al. 1884 | *D. pirina* P et al. 1884      | Wollenweber & Reinking (1935)                | *F. minutissima* Pirotti & Riboni                 | = Fusarium                            |
| Septorella Allesch. 1897 | *S. salicace Allesch. 1897      | Hühnel (1912)                                 | Unknown                                           | Status uncertain                     |
| Trichosporum Bubak 1906 | *T. rudis* Bubak 1906 ≡ *Fusarium roseum* var. *Sacc. 1886 | Wollenweber & Reinking (1935), Duke (1986)| *F. oxysporum* complex                            | = Fusarium, Dawk. & Punith. (pers. comm.) |
| Ustilaginoideella Essed 1911 | *U. musaeperda* Essed 1911      | Brandes (1919)                                 | Unknown                                           | Status uncertain                     |
| Stagonospora Desm. 1830 | *S. dulcamarae* Desm. 1830 : Fr. | Sutton (1977)                                 | *F. oxysporum* complex                            | = Fusarium, Henningsii 1993          |
| Fusantopas Horta 1919 | *F. demini Horta* 1919           | Dodge (1935)                                  | Unknown                                           | = Fusarium, Henningsii 1993          |
| Discosporum Petch 1921 | *D. tasmaniana* (McAlpine) Petch 1921 ≡ *Fusarium tasmanicum* McAlpine 1921 | Roosman (1983) | "Fusarium" anamorph of "Nectria" coccodaphaga (Pech) Rossman 1983 | = Fusarium, Henningsii 1993          |
| Pseudomicrocera Petch 1921 | *P. henningsii* (Koord.) Petch 1921 | Wollenweber & Reinking (1935)                | Microcera *dioica*                                | = Microcera, this paper              |
| Fusidomus Grove 1929 | Not designated                    | Sutton (1977)                                 | Unknown                                           | Status uncertain                     |
| Infurfagrus Cil. 1951 | *I. microsporus* (Sacc.) Cil. 1951 | Wollenweber & Reinking (1935)                | *Fusarium lateritium* complex                      | = Fusarium                            |
| Euryco B. & H. Maia 1955 | *E. domingueysi* B. & H. Maia 1955 | Summerbell & Schroers (2002)                  | *F. solani* complex                                | = Fusarium                            |
| Hyalofusarium B. & H. Maia 1955 | *H. ramosa* B. & H. Maia 1955     | W. Gams (pers. comm.)                         | *F. solani* complex                                | = Fusarium                            |
| Pseudofusarium Matsush. 1971 | *P. fusacidium* Matsush. 1971     | Pascoe (1990)                                 | *F. semitectum* auct.                             | = Fusarium, Matsushima 1980          |
| Pycnofusarium Punith. 1973 | *P. ruscii* D. Hawksw. & Punith. 1973 | Sutton (1986)                               | Pycnofusarium ruscii                               | = Trichosporum, Schroers (pers. comm.) |

and *Cylindrocladium*, the latter now treated by its teleomorph generic name, *Calonectria* (Lombard et al. 2010). Often, macroconidial anamorphs are accompanied by microconidial, *Acremonium*-like synanamorphs, with small ameroconidia produced from phialides and enveloped in slime. These are probably also plesiomorphic in the family and homologous to similar "microconidial" anamorphs in other families of the order. In some lineages, macroconidia seem to have disappeared, while in other lineages, microconidia seem to have disappeared. Verticillate anamorphs occur in some clades, in particular *Chaetopsis* and *Mariannaea*, presumably derived from *Acremonium*-like progenitors. In addition to micro- and macroconidia, mesoconidia have been described in a few species of *Fusarium* (Pascoe 1990) as intermediate between micro- and macroconidia, but dry and produced from holoblastic conidiogenous cells, while mecoconidia were described by Crous & Seifert (1998) in a few species of *Calonectria*, significantly larger than macroconidia and produced only under some cultural conditions.

*Fusarium*-like conidia occur in several orders of *Ascomycota* (Seifert 2001). In the *Nectriaceae*, the phylogenetic distribution of this character is disjunct. Because the phylogenetic backbone of the family is weakly supported in most analyses including ours, there are two possible interpretations for the distribution of the *Fusarium*-like conidium. If the *Fusarium*-like conidium is plesiomorphic in the *Nectriaceae*, then the cylindrical macroconidia of *Calonectria* and *Neonectria* were derived from it, and the taxa delimited by the ancestral *Fusarium*-like conidium have become paraphyletic. Alternatively, but perhaps less probable, the *Fusarium*-like conidium has evolved several times in the family, and the taxon delimited by this character is polyphyletic.

A practical problem with dividing *Fusarium* is the existence of 22 generic names sometimes considered synonyms (Table 2). These names must be considered in any division of the genus, which means that the identities of their type species in modern terms must be understood. Many of the synonyms come from the work of Wollenweber, whose herbarium studies are largely documented in his series *Fusarium autographice delineata* (Wollenweber 1916). Unfortunately, Wollenweber did not rigorously employ a type concept that conforms with today’s standards, and we have discovered that many of his interpretations cannot be verified. The status of some of the 22 synonyms can be evaluated on the basis of existing knowledge and we examined type specimens of relevant genera for this study (Table 2); the precise status of a few of these genera remains uncertain. We focused on older generic synonyms, seriously considering *Atractium* (1809), *Microcera* (1848), *Pionnotes* (1849), and *Fusicolla* (1851).
We considered two scenarios to resolve the para/polyphyly of Fusarium. The first was to adopt broad generic concepts and to maintain the two main lineages as genera, i.e. the terminal lineage including the type species of Fusarium, and the basal Fusarium-like lineage that includes most of the species attributed to Cosmospora sensu Rossman. The perithelial walls of the species of these two clades have clearly different micromorphology. Cultures generally differ in colony morphology and growth rates, produce different metabolites, and the species have different ecological preferences, especially host specificity. However, this separation was unsatisfactory because these two large clades themselves lacked convincing statistical support, and the amount of morphological diversity incorporated in both of these large clades was huge, rendering the resulting taxonomy meaningless from a practical point of view. In particular, the generic name Cosmospora would be supplanted by the oldest available name Microcera, resulting in a genus incorporating many large, phylogenetically well-supported clades, some of which are sufficiently well-defined ecologically and morphologically to be recognised as distinct genera on their own. In this broad concept of Microcera, anamorphs with Fusarium-like macroconidia would still not be monophyletic, because of the existence of a large clade of microconidial, Acremonium-like anamorphs that is terminal within this basal clade. The second option was to adopt the genera as well-supported, ecologically or morphologically distinct clades within the basal lineage. Although this results in more genera, the concepts are more homogenous and the system is practical. We followed this second approach, and the details of the generic names adopted are included in the Taxonomy section below. Fortunately, we were able to assign existing generic or subgeneric taxa to most of the clades. Cosmospora is retained for the clade with Acremonium-like microconidial anamorphs, and Microcera is reintroduced in something similar to its nineteenth century delimitation, as a genus of insect pathogens producing striking, flame-like conidiomata, especially host specificity. However, this separation was unsatisfactory because these two large clades themselves lacked convincing statistical support, and the amount of morphological diversity incorporated in both of these large clades was huge, rendering the resulting taxonomy meaningless from a practical point of view. In particular, the generic name Cosmospora would be supplanted by the oldest available name Microcera, resulting in a genus incorporating many large, phylogenetically well-supported clades, some of which are sufficiently well-defined ecologically and morphologically to be recognised as distinct genera on their own. 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Despite the number of genera segregated, this revision keeps the core of common, economically important Fusarium species intact. Of the species included in the popular Nelson et al. (1983) system and its more speciose successor (Leslie et al. 2006), only the F. aquaeductuum and F. mersmoides species complexes are removed to Fusicolla. The more difficult decision concerning the generic fate of the Fusarium solani species complex remains to be decided. Both Gams & Nirenberg (1989) and Seifert (2001) emphasised the importance of delimiting genera using polythetic concepts, i.e. concepts based on the occurrence of variable sets of shared characters with no single character considered essential for inclusion. Although we provide preliminary descriptions below, the development of robust polythetic diagnoses for the genera remains a work in progress. This is just the beginning of a taxonomic reevaluation of Fusarium and morphologically similar genera that, with increased sampling and more genomic analysis, will result in the recognition and definition of additional segregate genera. This revision provides a foundation for the discovery and phylogenetic classification of a large amount of presently unrecognised diversity representing both holomorphic and anamorphic species. It is unfortunate that our decision to attempt to implement a single name nomenclature to these fungi coincides with what may be equally a controversial decision to split Fusarium. In general, Fusarium workers have had little interest in teleomorphs and most will have no reluctance to abandon a dual nomenclature of little relevance to them. Because teleomorphs are rarely seen in culture, except for that of F. graminearum, they are considered the domain of taxonomic specialists and their nomenclatural primacy is an historical annoyance. The introduction of single scientific names for polythetically characterised holomorphs and the recognition of a single nomenclaturally valid name for all taxonomic ranks seem inevitable steps towards the stabilisation of fungal taxonomy (Rossman & Samuels 2005). We encourage mycologists to accept our proposed nomenclature as a sincere attempt to provide a functional single-name system that respects the principles of the ICBN and refrain from attempting to perpetuate a dual nomenclatural system where it is unlikely to be used by most scientists working on the practical aspects of these fungi.

**TAXONOMY**

In this section, we consider the classification, nomenclature, and typification of the species examined in our phylogenetic studies and implement the taxonomic conclusions discussed above. Where possible, we have examined holotype specimens, other authentic material, and/or ex-type cultures, as well as material conforming to the concepts of Wollenweber. When feasible, we designate lectotype or epitype specimens to stabilise species concepts and provide living material for further studies. Many species are pleomorphic having a teleomorph, a macroconidial, Fusarium-like anamorph, and a microconidial or Acremonium-like anamorph, or any combination of these. The morphs recorded for each species are indicated on Fig. 1. The species are not redescribed here. In some cases, species concepts applied by various authors deviate from the strict concept of the species as typified. Therefore, we refer only to descriptions and illustrations already published that represent the species indicated by the typification.

**Atractium Link** : Fr., Mag. Ges. naturf. Freunde, Berlin 3: 10 (tab. I, fig. 11), 1809 : Fries, Syst. Mycol. 1: xli, 1821.

**Type species:** *Atractium stilbaster* Link 1809.

**Emended generic diagnosis**

Teleomorph unknown. Conidiophores aggregated into sporodochia or synnemata, nonstromatic; in culture, sometimes becoming pionnotal. When produced synnemata determinate, pale brown, composed of a stipe of parallel hyphae and a divergent cap of conidiophores giving rise to a slimy conidial mass; differentiated marginal hyphal hyphae absent. Conidiophore branching once or twice monochasial, 2-level verticillate, monoverticillate or irregularly biverticillate. *Conidigenous cells* monophiloid, hyaline, subulate, with conspicuous periclinal thickening. Conidial masses yellow to orange. *Conidia* (0–)1–5-septate, clavate, obvoid or gently curved, rarely ellipsoidal, with a rounded apical cell, and somewhat conical basal cell, lacking a differentiated foot. *Chlamydospores* produced in culture by some species. Cultures growing relatively slowly, usually less than 30 mm diam in 14 d, with little aerial mycelium.

One of the commonly cited synonyms of *Fusarium* is the name *Atractium*, described immediately following and on the same page as its more famous cousin. The original diagnosis for *Atractium* and its type species *A. stilbaster* reads:

*Atractium*. Stromata elongatum, capitatum. *Sporidia fusiformia, non septata, capitulo instrata*. Stromata stibiformia, sporidia eadem quae Fusidiorum. Contextus stromatis, ut videtur, tenue floccosus, fioecassum paralleliss. Capitulum sub microscopicó compostó, aqua
adfusa, in sporidia fere differfnt. Unica species, nondum descripta. A. stilbaster, stipite cylindrico, capitulo globoso, utroque glabro lutescente. In truncis fagorum caesorum occurrit, vix ulta ½ lin. longa, fugax, stipite facili evanescente et capitulo in sporidia diffliente. Rarius invenit am. Ditmar. Iconem v. fig. 11."

The protologue includes a drawing by Ditmar (reproduced here as Fig. 2B), which shows what could either be a capitae, synnematous fungus, similar to Stilbella or possibly a myxomycete with a ruptured sporangium as seen in species of Trichia and many other genera, growing on a stump of Fagus. Link was confused about the septation of conidia of A. stilbaster. The protologues for both Fusarium and Atractium explicitly state, "Sporidia fusiformia, nonseptata...". Link (1816) added two more species to Atractium that Nees (1817) transferred to Fusarium without explanation. Link (1825) adjusted his observation and reported septate conidia in A. stilbaster, transferring it to Fusarium, and implicitly modifying his original species concept, and thus the generic concept of Atractium, to include species with septate conidia. These reinterpetations led subsequent authors, such as Berkeley, Fuckel, and Saccardo, whose systematic philosophy would not allow synnematous species to be included in the sporodochial genus Fusarium, to place synnematous Fusarium-like species in Atractium. In the 19th century, the prevailing concept of Atractium evolved to represent pale or colourful synnematous fungi with slimy conidial masses, usually with falcate, septate conidia. Tulasne & Tulasne (1861, 1865) noted the similarity of Atractium and Microcera (reintroduced below), and Petch (1921) commented on the modification of Link’s original concept to include species with septate conidia. The species added to Atractium were often associated with the teleomorph genus Sphaerostilbe, the species of which were revised by Seifert (1985a). Following the work of Wollenweber & Reinking (1935), who equated A. stilbaster with Fusarium aquaeductuum var. medium (now Dialonectria ullevolea, see below), Atractium was usually listed as a synonym of Fusarium. The proposed synonymy is curious because this species does not produce synnemata, the dominant feature of Link’s drawing of A. stilbaster. There is no reason to follow Wollenweber & Reinking’s interpretation and no evidence that Wollenweber, in his work for either Die Fusarien or Fusarium autographice deliniata, saw authentic material of A. stilbaster.

We were unable to locate authentic material of A. stilbaster, the original species of Atractium, from the herbaria of Link (B), Persoon (L) or Fries (UPS, UPS-Fries). The drawing with the protologue must be regarded as the lectotype; it shows what we interpret as a capitae, synnematous fungus (Fig. 2). The confusion over whether or not the conidia were septate, described above, is instructive in the interpretation of the identity of this fungus. To fix the application of the name, an epitype specimen should be designated of a synnematous fungus occurring on wood of Fagus in Germany. Seifert (1985a) provided a description and illustration of a fungus he called Stilbella fusca, a common, synnematous fungus on water-saturated, decayed wood, including trunks of Fagus, in northern Europe including Germany. It is the most frequently collected species attributed to the pre-1985 concept of Didymostilbe, and was often reported as D. eichleriens. This species produces slimy, obovate to oblanceolate conidia that are usually curved, from long phialides on branched conidiophores. The present concept includes species with predominantly asseptate conidia, but most specimens have only 1-septate conidia (Seifert 1985a). This species thus matches both Link’s original concept and his subsequent revised concept of A. stilbaster in all salient details, especially noting that other authors included it in Atractium. A culture of this fungus isolated from bark in Germany, CBS 410.67, is thus selected as the epitype for A. holubovae for this clade identified in Fig. 1.

The three species of Atractium accepted here are all associated with water in some way. Atractium stilbaster and A. holubovae (not known in culture) are associated with water saturated decaying wood, and A. crassum was isolated twice from drinking water in Germany.

In our phylogenetic analysis (Fig. 1), two species (A. stilbaster and A. crassum) form a well-supported monophyletic clade in the Nectriaceae. The clade is also basal to Chaetospina, Pseudonectria, and Volutella as discussed below.

We did not attempt a systematic reevaluation of the 24 species attributed to Atractium, but a summary of present knowledge is presented in Table 3.

No telemorphs are conclusively known for this genus, and there are no other published names that could be applied to this clade. Seifert (1985a) discussed the association of A. stilbaster with "Nectria" flavoviridis and Sphaerostilbe fusca, concluding that the reported association of this telemorph and anamorph was probably coincidental. Our reexamination of the type material suggests that the KOH– perithecia on the specimen are more likely to represent the telemorph of a species of Fusiciola, the macroconidia of which also occur on the specimen, rather than the telemorph of A. stilbaster.

KEY TO ACCEPTED ATRACTIUM SPECIES

1. Conidia mostly (0–1)–3 septate; synnematous conidiomata produced ................................................................. 2
2. Conidia mostly 3(–5) septate; synnemata not produced .............................................................................................. A. crassum

2. Conidia 37–49 × 4–5.5 μm; phialides 30–54 × 1.5–2.5 μm .......................................................................................... A. holubovae
2. Conidia 15–25 × 2–4.5 μm; phialides 20–40 × 1.5–2.5 μm .......................................................................................... A. stilbaster
Table 3. Species attributed to Atractium and their current status. Basic nomenclatural data from Index Fungorum (www.indexfungorum.org).

| Species, authority and year of publication | Status | Reference |
|------------------------------------------|--------|-----------|
| A. aurantiacum (Corda) Bonord. 1851       | Known  |           |
| A. brunaudiadana Sacc. 1883               | Known  |           |
| A. candidii Sacc. 1883                    | = Cylindrocarpon candidicum (Sacc.) Wollenw. |           |
| A. ciliatum Link 1816                    | Basionym of *Fusarium*ciliatum (Link) Link | This paper |
| A. cristatum Demelius 1923                | Unknown |           |
| A. cronartioides Spec. 1883               | Unknown |           |
| A. flammelum Höhn. 1915                  | Nomen dubium | Seifert 1985a |
| A. flavovirete Berk. & Ravenel 1854       | = Microcera coccophila Desm. | This paper |
| A. flavovirete Sacc. 1883                 | Synonym of A. stilbaster | Seifert 1985a |
| A. fuscum Sacc. 1883                     | Synonym of A. stilbaster | Seifert 1985a |
| A. gelatinosum (Pers.) Sacc. 1886         | No type in L, nomen dubium | Seifert 1985a |
| A. indicum Chona & Mujial 1956            | Unknown |           |
| A. lusitanicum Sousa da Câmara & Luz 1941 | Unknown |           |
| A. micropus (Pers.) Sacc. 1886            | No type in L, nomen dubium | Seifert 1985a |
| A. olivaceum Kunze & J.C. Schmidt 1817   | No type in B, nomen dubium | Seifert 1985a |
| A. pallens Nees 1818                     | Type in B examined, is a coelomycete | This paper |
| A. pallidum Bonord. 1851                 | Unknown |           |
| A. pallidum Berk. & M.A. Curtis 1868     | Unknown |           |
| A. pulvinatum Link 1816                  | Type in B examined, not an Atractium | This paper |
| A. rigidum Bonord. 1864                   | Unknown |           |
| A. stilbaster Link 1809                  | Accepted species | This paper |
| A. therr UNIT 1879                      | Anamorph of Demeria morthieri (Fuckel) Nannf. | Groves 1946 |
| A. trematis Hansf. 1944                  | Unknown |           |
| A. tubericola Sacc. & Pegion. 1902       | Unknown |           |

Accepted species

Atractium stilbaster Link 1809, Mag. Ges. naturf. Freunde, Berlin 3: 10.
Basionym: *Fusarium* stilbaster (Link) Link in Willdenow, Sp. pl., Edn 4 (2): 106. 1825 (4.24).
≡ Stilbella fusca (Sacc.) Seifert, Stud. Mycol. 35: 77. 1985.
See Seifert (1985a, as Stilbella fusca) for other synonyms.
Typification: Illustration published in Mag. Ges. naturf. Freunde, Berlin 3 as tab. I, fig. 11, lectotype designated here, reproduced here as Fig. 2B. Epitype of A. stilbaster designated here: Germany, Bayrischer Wald, Rachelseewand, on bark, Jul. 1967, W. Gams, CBS 410.67.
Other material examined: See Seifert (1985a), Canada, Quebec, Gatineau Park, Lac Bourgeois, on cut end of stump, Jul. 1992, K.A. Seifert, DAOM 215627.

Notes: Seifert (1985a) provided illustrations and a complete description of this species. The variability in conidium dimensions and septation reported by Seifert (1985a) may indicate the existence of several closely related but possibly morphologically diagnosable species.

Atractium crassum (Wollenw.) Seifert & Gräfenhan, comb. & stat. nov. MycoBank MB519420.
Basionym: *Fusarium merismoides* var. crassum Wollenw., Fus. autogr. del. 3: 857. 1930. (The publication of the same species in Zeitschrift für Parasitenkunde 3(3): 308. 1931 was apparently after the cited 1930 publication).
Typification: Germany, Berlin, isolated from drinking water, 1928, H.W. Wollenweber 3119, lectotype designated here, CBS. Ex-type cultures CBS 180.31 = NRRL 20894. GenBank barcodes: HQ897722 (rpb2), HQ897859 (aol1).
Notes: This species was described and illustrated by Wollenweber (1930, reproduced here as Fig. 2A), Wollenweber & Reinking (1935), and Gerlach & Nirenberg (1982). The strains described by the latter authors are now degenerated, and the following details come from their description. Fresh cultures grow slowly, 15–30 mm diam after 10 d on PDA, and sometimes produce *Coronium*-like structures. The macroconidia are generally curved around somewhat conical basal cell and a rounded apical cell; there is no foot to the basal cell. They are mostly 3–5-septate; 3-septate conidia average 52 × 5 μm (ranging 37–60 × 4.5–5.5), 4–5-septate 60 × 5.5 μm (50–65 × 5.6), 1–2 septate 31 × 4.5 μm (25–37 × 3–6). Chlamydospores are terminal, intercalary or in conidia, round, 7–12 μm diam.
A second culture, BBA 62257, was illustrated by Gerlach (1972) and Gerlach & Nirenberg (1982) but is no longer available. A dried culture kept in the CBS herbarium is designated as lectotype above, because it is the only known original material. Wollenweber’s published illustration of the type strain (Fig. 2A) represents the macroconidia of this taxon well. Epitypification must await the isolation of a fresh culture and specimen that can demonstrate the salient morphological features more completely than the existing cultures.
This species developed in damp chambers on small twigs collected from cold, running river water in Ontario, Canada, but the cultures were not preserved and the fungus cannot be relocated on the original specimen. Attempts to recollect and reisolate the fungus from the same locality were unsuccessful. The conidiomata on the natural substrate were glistening white and flame-shaped; the bundles of parallel macroconidia give the appearance of minute synnemata (Fig. 2C). However, little conidiomatal tissue is actually produced, and the phialides arise from a typical, Fusarium-like sporodochium of interwoven but not stromatic hyphae and conidigenous cells.

Atractium holubovae (Seifert, S.J. Stanley & K.D. Hyde) Seifert, comb. nov. MycoBank MB519421.
Basionym: Stilbella holubovae Seifert, S.J. Stanley & K.D. Hyde, Sydowia 47: 258, 1995.
Typhification: Philippines, Negros Occidental, Bario Caliban, Caliban River, on submerged wood, Dec. 1994, K.D. Hyde & E. Arnas, holotype DAOM 214961.

Notes: This species was described and illustrated by Seifert et al. (1995) in the absence of pure cultures and is transferred here on the basis of its morphological similarity with A. stilbaster. It is known from the holotype and two subsequent records on submerged wood collected from streams in Asia (Sivichai et al. 2002, Fryar et al. 2004).

Cosmospora Rabenh., Hedwigia 2: 59. 1862.

Type species: Cosmospora coccinea Rabenh. 1862.

Stroma inconspicuous or absent. Perithecia scattered to gregarious, pyriform with an acute or apical papilla, collapsing cupulate or pinched when dry, orange red or bright red, turning dark red in KOH+, smooth walled, usually 150–450 μm high. Asci cylindrical to narrowly clavate, with an apical ring, 8 uniseriate or partly biseriate ascospores. Ascospores initially hyaline but becoming yellow brown to reddish brown, 1-septate, becoming tuberculate when mature. Conidiophores Acremonium-like, either lateral phialides on somatic hyphae, or with one or two layers of monochasial branching, or verticillate, hyaline. Phialides monophialidic, cylindrical to subulate, hyaline. Microconidia ellipsoid, oblong or clavate or slightly allantoid, aseptate, hyaline, in slimy heads. Macroconidia absent. Chlamydospores usually not seen, but produced on some media.

Colonies on PDA slow growing, 15–25 mm diam in 14 d at room temperature, surface powdery, felt-like, floccose, cottony, white, pale pink, ochre to olivaceous green, sporulation usually abundant, arising directly from agar surface or from sometimes abundant aerial mycelium.

Habitat: On fruiting bodies and stromata of other fungi, e.g. Fomitopsis, Hypoxylon, Inonotus, Stereum, often isolated from soil.

Notes: About 65 species have been attributed to Cosmospora sensu Rossman. This concept is relatively broad, encompassing a great deal of anamorphic variability, although the teleomorph morphology is relatively conserved, with small, orange or reddish KOH+ perithecia with thin walls, cylindrical asci with or without an apical ring, and eight, uniseriate, 1-septate ascospores; stroma development is usually limited. Our phylogenetic analyses (Fig. 1) identify several distinct lineages within the prevailing concept of Cosmospora. New teleomorph genera have already been proposed for some lineages, namely Neotrichiadiella (a synonym of the anamorphically defined genus Cylindrocladiella) and Chaetopsisinecchia (a synonym of the anamorphically defined genus Chaetopsisina). In general, well-supported clades correlate with anamorph types, although Fusarium-like anamorphs are found in several lineages.

Here, we propose a more restricted concept for Cosmospora, limiting it to the clade of species surrounding the type, C. coccinea, which have only microconidial, Acremonium-like anamorphs and tend to occur on other fungi. Other microconidial genera recognised are Mariannaea and Volutella. The clades with Fusarium-like anamorphs are reclassified below in the reintroduced genera Dialonectria, Fusicolla, and Microcera, with Macroconia elevated to generic rank from its previous sectional rank in Nectria. A small residue of species remains in Cosmospora sensu Rossman that are not redissolved here.

Although several of the new combinations propose the transfer of an anamorph typified name to a teleomorphically typified genus, as explained in the Introduction, the results are correct, legitimate, and valid for those species that are not pleomorphic, i.e. those that lack a teleomorph and are outside Art. 59 of the ICBN.

Accepted species

Cosmospora coccinea Rabenh., Hedwigia 2: 59. 1862 [non Nectria coccinea (Pers.) Fr. 1849]. = Verticillium olivaceum W. Gams, Cephalosporium-artige Schimmelpilze, p. 129, 1971.

Typhification: Germany, near Laubach, on rotting poles of a polypropolyne, Solms. Fungi europaei no. 459, lectotype BPI designated by Rossman et al. 1999.

Other material examined: Germany, Bayrischer Wald, Arberseeawand, on hymenium of Inonotus nodulosus on Fagus sylvatica, Aug. 1967, W. Gams 680, CBS 341.70 = VKM F-2863; Kr. Plön, near Dobsersdorf, on hymenium of Inonotus radiatus on Alnus, Oct. 1965, W. Gams 1104, CBS 343.70; Effel, Geeser Wald near Gerolstein, on Inonotus radiatus, Sep. 1970, W. Gams, CBS 841.70; Effel, Geeser Wald near Gerolstein, on Inonotus radiatus, Sep. 1970, W. Gams, CBS 983.70 = VKM F-2862; Neubrandenburg, Keppelshager Forst near Friedland, on Inonotus radiatus, Oct. 1978, P. Häußch H78/40, CBS 704.79; Bayern, on Inonotus nodulosus, dead crust on fallen branch of Fagus sylvatica, 1993, T.R. Lohmeyer & R. Boesemiller 9362, A.R. 2741 = BPI 802729 = CBS 114050; Nordrhein-Westfalen, Detmold, Krebestich, on Inonotus nodulosus on Fagus sylvatica, Apr. 2007, T. Gräfenhan 2007-37, DAOM 235821.

Notes: For descriptions, illustrations, and additional taxonomic synonyms of the microconidial anamorph, see Gams (1971); the teleomorph is briefly described by Rossman et al. (1999).

Cosmospora arxii (W. Gams) Gräfenhan & Schroers, comb. nov. MycoBank MB519422.

Basionym: Acremonium arxii W. Gams, Cephalosporium-artige Schimmelpilze, p. 123. 1971.

Typhification: Germany, Niedersachsen, near Wilhelmshaven, Neuenburger Unwald, on Hypoxylon sp., May 1965, W. Gams, holotype CBS H-6635, ext-type culture CBS 748.69 GenBank barcodes: HQ897725 (rpb2), HQ897862 (αf1).

Other material examined: Germany, Nordrhein-Westfalen, Kamen, Heerender Holz, on Hypoxylon fagus, Apr. 2007, T. Gräfenhan 2007-22, DAOM 235822; Nordrhein-Westfalen, Detmold, Extermaine, on Hypoxylon on Fagus sylvatica, Apr. 2007, T. Gräfenhan 2007-28, DAOM 235823; Nordrhein-Westfalen, Detmold, Donoper Teich, on Hypoxylon on Fagus sylvatica, Apr. 2007, T. Gräfenhan 2007-29, DAOM 235824 & T.G. 2007-33, DAOM 235825; USA, Pennsylvania, near Salt Springs State Park, on Hypoxylon on Acer, May 2007, T. Gräfenhan 2007-55, DAOM 235826.

Notes: The teleomorph of Cosmospora arxii is commonly found on Hypoxylon spp. on Fagus in North America and Europe, but has not been described yet; its morphology is similar to that of C. viridescens. For a description, illustrations, and discussion of the microconidial anamorph, see Gams (1971) and notes under C. berkeleyana below.

Cosmospora berkeleyana (P. Karst.) Gräfenhan, Seifert & Schroers, comb. nov. MycoBank MB519423.

Basionym: Verticillium berkeleyanum P. Karst., Meddeland. Soc. Fauna Fl. Fenn. 18: 64. 1891.
≡ Acremonium berkeleyanum (P. Karst.) W. Gams, Nederlands J. Pl. Pathol. 86: 76. 1982.

Typhification: Finland, near Mustiala, on Stereum hirsutum on Betula, Oct. 1890, P.A. Karsten 2310, holotype H.

Notes: For a description and discussion of this microconidial species, see Karsten (1891) and Gams & Zaayen (1982).
Although some have considered the teleomorph to be the heterotopic Hypomyces berkeleyanus Plowr. & Cooke (≡ Sphaerostilbella berkeleyana (Plowr. & Cooke) Samuels & Candousau), our observations complicate the situation considerably. Because our phylogenetic results suggest that this is a species complex, the proposed synonyms applied to the teleomorph-anamorph connections forCosmospora berkeleyana need to be re-evaluated (Fig. 1). These synonyms include Acremonium butyri, Cephalosporium khandalense, Gliomastix lavitskiae, Nectria vilior, and V. viridescens (Gams 1971, Samuels et al. 1990. Rossman et al. 1999). In our phylogenetic analysis, all of these putative synonyms can be interpreted as distinct species of Cosmospora.

Cosmospora berkeleyana, C. vilior, and C. viridescens have often been considered synonymous, but this now seems unlikely and each name must be re-evaluated. Samuels et al. (1990, 1991) studied and discussed the type material of C. vilior on a valsaecous stroma from Brazil. Because no fresh material from subtropical South America is available, we are unable to reinterpret Samuels’ concept in phylogenetic terms. Cosmospora viridescens was described from a fungal host on Salix in Europe and thus may have distinct host relationships and geographical distribution. Possible morphological distinctions between these two teleomorphs are discussed below under C. viridescens.

Gams & Zaayen (1982) studied a recent specimen and culture identified as Acremonium berkeleyanum, which was unavailable for our study (The Netherlands, Oostelijk Flevoland, Abbert-bos, perceel O66, on Stereum hirsutum, July 1981, W. Gams, CBS 501.81). A similar fungus producing perithecia and the characteristic greenish Acremonium-like anamorph on basidiocarps of S. hirsutum on Alnus rubra is common in British Columbia, Canada (Seifert, unpubl. data).

Until species limits can be more clearly established, we prefer not to epitypify C. berkeleyana or C. vilior. The diversity of substrates and broad geographic distribution recorded for C. berkeleyana (Gams 1971, www.cbs.knaw.nl/databases) suggest that additional phylogenetic species await discovery in this complex.

Cosmospora butyri (J.F.H. Beyma) Gräfenhan, Seifert & Schroers, comb. nov. MycoBank MB519428.
Basionym: Tilachlidium butyri J.F.H. Beyma, Zentralbl. Bakteriol., 2 Abt. 99: 388. 1938.
≡ Acremonium butyri (J.F.H. Beyma) W. Gams, Cephalosporium-artige Schimmelpilze, p. 126. 1971.

Typification: Denmark, Copenhagen, butter, Knudsen, holotype CBS H-6601, ex-type cultures CBS 301.38 = MUCL 9950. GenBank barcodes: HQ897729 (rpB2), HQ897866 (acFl).

Notes: No teleomorph is known, but see notes under C. berkeleyana above. This microconidial species is described, illustrated, and discussed by van Beyma (1938) and Gams (1971). As noted by Summerbell et al. (2011), there may be more than one fungus preserved CBS 301.38; we have not examined the holotype specimen.

Cosmospora cymosa (W. Gams) Gräfenhan & Seifert, comb. nov. MycoBank MB519429.
Basionym: Acremonium cymosum W. Gams, Cephalosporium-artige Schimmelpilze, p. 131. 1971.

Typification: Germany, Schleswig-Holstein, Kr-Rendsburg, Eikendorfer Gehölz, on decaying Inonotus radiatus, Oct. 1965, W. Gams, lectotype designated here CBS H-5054, isotype CBS H-6603, ex-type culture CBS 762.69. GenBank barcodes: HQ897778 (rpB2), HQ897914 (acFl).

Other material examined: Germany, Kr-Plön, Dobersdorfer Wald, on Inonotus radiatius on Anthus glutinosus, June 1965, W. Gams 512A, CBS H-8146, CBS 258.70.

Notes: For description and illustrations of this microconidial anamorphic species, see Gams (1971). No teleomorph is known.

Cosmospora khandalensis (Thirum. & Sukapure) Gräfenhan & Seifert, comb. nov. MycoBank MB519430.
Basionym: Cephalosporium khandalense Thirum. & Sukapure, Mycologia 58: 359. 1966.

Typification: India, Maharashtra, Khandala, on decaying stem of Bambusa, Aug. 1964, M.J. Thirumalachar, holotype HACC 148, isotype CBS H-15076, ex-type cultures ATCC 16091 = CBS 356.65 = IMI 112790 = MUCL 7974. GenBank barcodes: HQ897723 (rpB2), HQ897860 (acFl).

Notes: The microconidial anamorph of this species as typified here is described and illustrated by Sukapure & Thirumalachar (1966) and discussed by Gams (1971). See notes above under C. berkeleyana.

Cosmospora lavitskiae (Zhdanova) Gräfenhan & Seifert, comb. nov. MycoBank MB519431.
Basionym: Gliomastix lavitskiae Zhdanova, Mikrobiol. Zhurn. 28: 37. 1966.

Typification: Ukraine, Poltawa region, on plant debris from rhizosphere soil of Zea mays, July 1961, holotype D.K. Zabolotny Institute of Microbiology and Virology of the National Academy of Sciences of Ukraine, ex-type cultures ATCC 18668 = CBS 530.68 = IMI 133984 = VKM F-1324. GenBank barcodes: HQ897726 (rpB2), HQ897863 (acFl).

Notes: The microconidial anamorph of the species is described and illustrated by Zhdanova (1966) and discussed by Gams (1971). No teleomorph is known. See notes above under C. berkeleyana.

Cosmospora viridescens (C. Booth) Gräfenhan & Seifert, comb. nov. MycoBank MB519432.
Basionym: Nectria viridescens C. Booth, Mycol. Papers 73: 89. 1959.

Typification: UK, England, Yorkshire, Sawley Woods, on black pyrenomycete on branches of Salix, Apr. 1954, C. Booth, holotype IMI 56736, isotype DAOM 83074.

Notes: The microconidial anamorph and teleomorph of this species as typified are described, illustrated, and discussed by Booth (1959) and Gams (1971).

Cosmospora viridescens is morphologically similar to C. vilior, but the latter has tuberculate ascospores, compared to the spinulose ascospores of C. viridescens (Samuels et al. 1990). Both species have Acremonium-like anamorphs with green colonies, and their perithecia occur on black, valsaecous stromata. Ascospore isolates made from perithecia collected on stromata of Hypoxylon and Ustulina in temperate areas often yield green colonies similar to C. viridescens, but are probably different from the tropical or subtropical species identified as C. vilior. Furthermore, differences in substrate specificity and geographic distribution support the distinction of C. viridescens from the other Cosmospora species mentioned above.

Cosmospora viridescens cannot be correlated with any described Acremonium species, nor can any of the described Acremonium species in this complex be unequivocally connected
to any of the described teleomorphic species. Of the species in this complex with names based on anamorphic types, only C. arxii unequivocally has a known teleomorph, but it has apparently never been named.

Dialonectria (Sacc.) Cooke, Grevillea 12: 109. 1884. MycoBank MB1491.

Type species: Dialonectria episphaeria (Tode : Fr.) Cooke 1884 as D. sanguinea

Stroma inconspicuous or absent. Perithecia scattered and solitary or in small groups, pyriform with a short acute or round apical papilla, collapsing cupulate or pinched when dry, orange red to carmine red, turning dark red in KOH+, smooth-walled, usually < 200 μm high. Ascii cylindrical to narrowly clavate, with an apical ring, 8 uniseriate ascospores. Ascospores hyaline to pale brown, 1-septate, smooth or becoming tuberculate when mature. Conidiophores initially as lateral phialides on somatic hyphae, sometimes verticillate, hyaline. Phialides monophialidic, subulate to subclavate, hyaline. Microconidia ellipsoid to clavate, asceptate, hyaline, abundant. Macroconidia, if present, subhyaline, moderately curved, slightly narrowing toward each end, apical cell often slightly hooked with a more or less pointed tip, basal cell not or scarcely pedicellate, predominantly 3–5-septate, hyaline, mostly thin-walled. Chlamydospores not observed.

Colonies on PDA slow growing, 25–50 mm diam in 14 d at room temperature, surface smooth, white to orange, aerial mycelium sparse, often becoming pionnotal, i.e. with abundant sporulation occurring in slimy masses over colony surface, often without discrete sporodochia.

Habitat: Mostly growing on stroma of other ascomycetes on deciduous trees.

Notes: Dialonectria was introduced first as a subgenus of Nectria and was revised in that context by Samuels et al. (1991), with a delimitation that more or less correlated with what the same authors later assigned to Cosmospora sensu Rossman. With the more restricted delimitation of Cosmospora adopted above, we also propose a restricted concept of Dialonectria around its type species, D. episphaeria. Most of the ~45 other species ascribed to Dialonectria by various authors have been reassigned or synonymised with other species by students of Nectria over the past 30 years.

Several phylogenetically distinct lineages are known within the D. episphaeria complex, one of which is described as a new species below.

Accepted species

Dialonectria episphaeria (Tode : Fr.) Cooke as D. sanguinea, Grevillea 12: 110. 1884.

Basionym: Sphaeria episphaeria Tode : Fr., Tode, Fungi Mecklenb. Sel. 2: 1791: Fries, Syst. Mycol. 2: 454. 1823.

≡ Nectria episphaeria (Tode : Fr.) Fr., Summa Veg. Scand. 2: 388. 1846.
≡ Cucurbitaria episphaeria (Tode : Fr.) O. Kuntze, Rev. Gen. Plant. 3: 461. 1893.
≡ Fusarium episphaeria (Tode) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 22: 662. 1935.
≡ Cosmospora episphaeria (Tode : Fr.) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 121. 1999.

Notes: For description, illustrations, and discussion of the teleomorph, see Booth (1959). The anamorph produces micro- and macroconidia and is described by Gerlach & Nirenberg (1982) and Nelson et al. (1983).

The morphological species Dialonectria episphaeria splits into at least five phylogenetic lineages, which share similar phenotypic traits (Gräfenhan et al. 2008). There is presently no fresh, well-characterised material on Diatype on Crateagus from northern Germany suitable for epitypification. The anamorph of D. episphaeria was often reported as or referred to as Fusarium aquaeductuum var. medium, e.g. Gerlach & Nirenberg 1982, but we consider this to represent a different phylogenetic species that is described below as a new species.

Dialonectria ullevolea Seifert & Gräfenhan, sp. nov. MycoBank MB519433. Fig. 3A–J.
≡ Fusarium aquaeductuum var. medium Wollenw., Fus. autogr. del., no. 844. 1930.

Etymology: K.A.S. recalls impassioned discussion on the topic of dividing Fusarium with P. Crous, K. O’Donnell, M. Stadler, and B. Summerell during the 7th International Mycological Congress in Oslo, Norway, August 2002; this is commemorated with Dialonectria ullevolea, named for the Ullevol pub, where this discussion occurred.

Colonies in agar CMA perithecia fertile, aurantiaco-rubra vel rubra formantes; perithecia pyriforma, papilla brevis praedita, Dialonectiae episphaeriae similia, ascosporis dilute brunneis, bicerullatibus, (8.7–)9.7–11–(12.5) × (3.7–)4.5–(4.8) μm. Conidiophora primum phialides simplices ex hyphis orientes, deinde irregulariter verticillatae. Phialides arising laterally from hyphae, later irregularly or occasionally verticillately branched. Phialides monophialidic, subulate to subclavate, 8–20 × 1.5–2.3 μm, hyaline. Conidiophores initially unbranched, with abundant sporulation occurring in pionnotal masses on single conidiophores, delicate, floccose spots, lacking or appressed at margin. Aerial mycelium sparse or occasionally with floccose spots, lacking or appressed at margin. Sporulation in orange pionnotal masses, first observed near colony centre. Sclerotial bodies not observed.

On CMA, the type culture forms fertile, orange red to bright red perithecia, pyriform each with a short apical papilla, morphologically similar to Dialonectria episphaeria as described by Booth (1959); ascospores pale brown, 1-septate, (8.7–)9.7–11–(12.5) × (3.7–)4.4.5–(4.8) μm (n = 50).

Colonies slow-growth on PDA, 25–30 mm diam in 14 d at room temperature. Surface light orange (5A5) to greyish orange (5B5) in colony centre, whitish at margin, margin smooth to broadly lobed. Reverse similar in colour but less bright with a slightly yellowish tinge (6A4 to 6B5). Aerial mycelium sparse or occasionally with floccose spots, lacking or appressed at margin. Sporulation in orange pionnotal masses, first observed near colony centre. Sclerotial bodies not observed.

In culture on CMA: Conidiophores initially unbranched, with phialides arising laterally from hyphae, later irregularly or occasionally verticillately branched. Phialides monophialidic, subulate to subclavate, 8–20 × 1.5–2.3 μm, hyaline. Conidia produced abundantly in pionnotes of aggregated conidiophores or on single conidiophores, delicate, hyaline. Microconidia ellipsoidia clavate, aseptate, (3–)3.5–5–(6.5) × 1–1.5–(1.7) μm (n = 30), hyaline, abundant. Macroconidia subcylindrical, moderately curved, slightly narrowing toward each end,
apical cell often slightly hooked with a more or less pointed tip; basal cell not or scarcely pedicellate, predominantly 3–5-septate, 1-septate: 10–25 × 1.5–2 μm (n = 5), 3-septate: (20–)30–42(–48) × (1.8–)2–2.5(–2.7) μm (n = 40), 4–5-septate: (30–)37–43.5(–50) × (1.8–)2–2.5(–2.7) μm (n = 30), 6–7-septate: 40–48(–52) × (2–)2.3–2.7 μm (n = 25). Chlamydospores not observed.

**Typification**: Netherlands, Baarn, Groeneveld, perithecia on branch of Fagus sylvatica, July 1984, K.A. Seifert 357, holotype CBS H-3565, ex-type cultures BBA 64549 = CBS 512.84 = NRRL 20688. GenBank barcodes: HQ897749 (rpb2), HQ897885 (acl1).

**Other material examined**: USA, Pennsylvania, near Salt Springs State Park, on pyrenomycete stroma on Fagus, May 2007, T. Gräfenhan 2007-56, DAOM 235827; Canada, Quebec, Mayo, Forêt la Blanche, on pyrenomycete stroma on deciduous tree, Oct. 2007, T. Gräfenhan 2007-72, DAOM 235828.

**Notes**: To preserve the taxonomic concept of *F. aquaeductuum* var. *medium sensu* Wollenweber (1930), we typify *Dialonectria ullevolea* with an isolate from *Fagus sylvatica* collected in The Netherlands. The species produces a teleomorph and both microconidial and macroconidial synanamorphs; it seems to be pan-temperate and has been collected in Europe and North America.
Fusicolla Bonord., Handbuch der allgemeinen Mykologie p. 150. 1851.

Type species: Fusicolla betae (Desm.) Bonord. 1851.

Stroma erumpent from host with hyphae forming a slimy, pale orange sheet over the substratum, with perithecia fully or partially erumpent from host with hyphae forming a slimy, pale Stroma.

Accepted species

Fusicolla betae (Desm.) Bonord., Handbuch der allgemeinen Mykologie p. 150. 1851. Fig. 4.

Basionym: Fusisporium betae Desm., Ann. Sci. Nat., Bot., Sér. 1, 19: 436. 1830.

≡ Fusarium betae (Desm.) Sacc., Michelia 2: 132. 1880.
≡ Pionnotes betae (Desm.) Sacc., Syll. Fung. 4: 726. 1886.
≡ Pionnotes rhizophila var. betae (Desm.) De Wild. & Durieu, Prodr. Fl. Belg. 2: 367. 1898.

Colony on PDA slow growing, 30–55 mm diam in 14 d at room temperature, surface smooth, whitish to pale brown, pink or orange, sometimes with violet or reddish-brown tones, often entirely pionnotal; **aerial mycelium** sparse or abundant, turf-like, felt-like, or coremioid if with violet or reddish-brown tones.

Habitat: On soil or plant matter in contact with soil, on woody material, slime flux of trees, sometimes on stromata of other fungi, in flowing water including drinking water and sewage.

Notes: Morphologically, Fusicolla betae closely resembles other members of the Fusicolla merismoides species complex, and critical taxonomic reevaluation of this complex is required to develop reliable species concepts.

There has been confusion over the identity of this species with two independent concepts in the literature. Wollenweber (1916, see below), six of them by Karsten. We have not seen the type specimens of any of these species, which have apparently not been revised since their original descriptions.

Other material identified: Germany, northern Germany, rotting potato tuber, E. Langerfeld DE 6, FRC E-0114 = MRC 2196 = NRRL 47196. Turkey, roots of Papaver, 2007, G. Turhan, T.G. 2007-70. UK, on Beta vulgaris, IMI 105043 = NRRL 22133.
was usually listed as a synonym of Fusarium, e.g. Carmichael et al. 1980. Alternatively, Chupp (1954, p. 111) cited Fusarium betae and “Fusidium betae Desm.” (probably a lapsus for Fusisporium) as synonyms of Cercospora beticola. He cited only the type of C. beticola and types of other Cercospora names synonymised with C. beticola; types of the Fusarium/Fusidium names were not cited. We conjecture that he proposed the synonymy based on the identity of the host and a general congruence in conidial size and septation. Crous & Braun (2003) followed the latter synonymy name on the identity of the host, and a general congruence in conidial size and septation.

Wollenweber noted the presence of two aqueductuum 47231, FRC E-0288 = NRRL 47232. E-0205 = NRRL 47210, FRC E-0226 = NRRL 47215, FRC E-0229 = NRRL 47844, south Africa 175962 = NRRL 22137. These species produce sporodochia, phialides, and of the lectotype designated above confirm that Desmazières' fungus produces sporodochia, phialides, and Fusarium-like conidia identical to those of the epitype selected above.

Fusicolla acellulera (Tubaki, C. Booth & T. Harada) Gräfenhan & Seifert, comb. et stat. nov. MycoBank MB519434.

Basionym: Fusarium merismoides var. acellulera Tubaki, C. Booth & T. Harada, Trans. Brit. Mycol. Soc. 66: 355. 1976.

Typification: Japan, Osaka, near Osaka University, soil, 1973, T. Miyoshi, holotype IFO 30040, ex-type cultures IMI 181468 = BBA 63789 = NRRL 20827. GenBank barcodes: HQ897701 (rpb2), HQ897839 (aof1).

Other material identified: Australia, soil, FRC E-0052 = NRRL 13261, FRC E-0120 = NRRL 47187, FRC E-0121 = NRRL 47188, ICMP 10485 = NRRL 39744, IMI 175962 = NRRL 22137. Philippines, Nueva Vizcaya, Faors, FRC E-0184 = NRRL 47201. South Africa, soil, FRC E-0130 = NRRL 47191, FRC E-0136 = NRRL 47193, FRC E-0205 = NRRL 47210, FRC E-0226 = NRRL 47215, FRC E-0229 = NRRL 47844, FRC E-0257 = NRRL 47222, FRC E-0265 = NRRL 47224, FRC E-0287 = NRRL 47231, FRC E-0288 = NRRL 47232, Zambia, soil, FRC E-0208 = NRRL 47212.

Notes: This species produces both macroconidia and microconidia. The holotype is described, illustrated, and discussed by Tubaki et al. (1976) and Gerlach & Nirenberg (1982).

Fusicolla aquaeductum (Radlk. & Rabenh.) Gräfenhan, Seifert & Schroers, comb. nov. MycoBank MB519435.

Basionym: Selenosporium aquaeductum Radlk. & Rabenh., Kunst- Gewerbe-Blatt 49: 10. 1863. = Fusarium aquaeductum (Radlk. & Rabenh.) Lagerh., Centralbl. Bakteriol. Parasitenk. B 655. 1891.

Typification: Germany, Bayern, München, water fountain near Gasteigstein, Nov. 1862, L. Radlkofer, lectotype designated here B 700014034. A permanent slide prepared by Radlkofer and sent to Wollenweber is selected here as the lectotype of Selenosporium aquaeductum; it is the only known authentic material. Epitype designated here: Germany, Berlin-Dahlem, Julius-Kühn-Institute (formerly BBA), iso. ex plugged water tap in BBA, May 1985, H.J. Nirenberg, ex-type cultures BBA 64559 = CBS 837.85 = NRRL 20865 = NRRL 37595. GenBank barcodes: HQ897744 (rpb2), HQ897780 (aof1).

Other material examined: Germany, Berlin, drinking water, 1974, W. Gerlach, BBA 63689 = CBS 734.79 = NRRL 20866. The Netherlands, Baarn, rubber tubing, 1963, A.L. van Beverwijk, CBS H-12677, CBS 268.53 = NRRL 22115.

Notes: No teleomorph is known for this species. For a description, illustrations, and discussion of the microconidial and macroconidial synanamorphs of this species as epitypified here, see Gerlach & Nirenberg (1982).

In Radlkofer (1863), two figures illustrate Selenosporium aquaeductum, one showing 1–2(–4)-septate conidia borne on phialides. Wollenweber (1916) studied a permanent slide originally prepared by Radlkofer and drew the fungus with 1-septate and 3–4-septate conidia. On the herbarium sheet with that slide, Wollenweber noted the presence of two Fusarium species, F. aquaeductum with 1-septate conidia, 18–22 × 1.5–2 μm and F. bialettiolianum with 3-septate conidia, 30–55 × 2–2.5 μm. Based on similarities of the phenotype and substrate preferences, we classify Fusarium aquaeductum in Fusicolla.

Wollenweber & Reinking (1935) included Microcera brachyspora Sacc. & Scal. as a synonym of F. aquaeductum, but this should be confirmed with type studies.

Wollenweber (1931) linked Fusarium aquaeductum var. aquaeductum to "Nectria" epispheira var. coronata (syn. "Nectria" purtonii, see below); subsequently this anamorph-teleomorph connection was accepted by Booth (1959), Gerlach and Nirenberg (1982), Samuels et al. (1991), and Rossman et al. (1999). According to our phylogenetic results, "Nectria" purtonii is not a member of Fusicolla but belongs to Stylonectria. The reported anamorph-teleomorph connection could not be confirmed here.

Fusicolla epistroma (Höh.) Gräfenhan & Seifert, comb. nov. MycoBank MB519436.

Basionym: Dendrodochium epistroma Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Wien, Math.-Naturwiss. Kl., Abt. 1, 118: 424. 1909. = Fusarium epistroma (Höh.) C. Booth as F. epistromum, The Genus Fusarium p. 66. 1971.

Typification: Germany, Brandenburg, "Schmidt's Grund" near Tamsel, on old stromata of Diatrypella favacea on branches of Betula, Nov. 1906, P. Vogel, Sydow's Mycotheca germanica 648 Hymenula epistroma, lectotype B 700014042 designated here, isotypes FH 00286649, K, S F40143. Epitype designated here: UK, England, Yorkshire, Airedale & Goulstone, on Diatrypella on Betula, Apr. 1961, C. Booth, IMI 85601, ex-type cultures ATCC 24369 = BBA 62201 = NRRL 20461 = NRRL 20439. GenBank barcodes: HQ697765 (rpb2), HQ897901 (aof1).

Other material examined: Germany, Triglitz, 1907, O. Jaap, herb. von Höhnel 3087, FH 00286650.

Notes: For descriptions, illustrations, and discussion of the micro- versus macroconidial synanamorphs of this species, see Booth (1971) and Gerlach & Nirenberg (1982).

An anamorph-teleomorph connection of F. epistromum with Nectria ("Cosmospora") magnusiana was suggested by Höhnel (1909) and later followed by Jaap (1910), Booth (1959), Gerlach & Nirenberg (1982), and Samuels et al. (1991). Höhnel (1909) based his assumption on the observation that both fungi occurred on the same host fungus, Diatrypella favacea. However, he did not collect or observe the teleomorph together with his Dendrodochium epistroma. Wollenweber (1924, No. 539) studied a specimen of N. magnusiana collected by Jaap (Fungi selecti exs. 418) and questioned the link with Höhnel's anamorphic fungus. Booth's (1959) report of the anamorph-teleomorph connection included a drawing of the anamorph that lacks attribution to a specimen, but looks much like Wollenweber's Fusaria autographice delineata no. 539. The conidiophores and conidia are similar, having subulate phialides and non-septate, oblong to allantoid conidia. We compared Rehm's type material (S F84956, B 700014041) to the description given by Samuels et al. (1991) based on Jaap's exsiccati. In contrast to the latter, the KOH– ascomatal wall of the type specimen appears slightly verrucose and the colour is dark orange-brown with an obtuse apex and an ostiolar area that becomes almost black. Mature ascospores of Nectria magnusiana measure (12–)13–14.5(–15.5) × (5.5–)5.8–6.5(–6.8) μm and are significantly wider than those of the Jaap exsiccata studied by Samuels et al. (1991). The type material of N. magnusiana is reminiscent of Neonectria or Nectria s.str. An anamorph was associated with the same stroma from which perithecia developed. Its buff-coloured hymenium bears oblong-ellipsoidal microconidia conidia, 3.5–8 × 1–2 μm. These microconidia...
match those observed in two authentic collections of *Dendrodochium epistroma* (Sydow’s Mycotheca Germanica 648 and Jaap’s Fungi Selecti Exsiccati 349). Booth (1939) and Samuels et al. (1991) concluded that *D. epistroma* is the anamorph of *N. magnusiana*, both being host specific to *Dia try pella favaecea*. Only a few *Fusarium*-like macroconidia were found on the type material of *Dendrodochium epistroma*, but macroconidia were lacking on the hynemum of the type collection of *N. magnusiana*. Interestingly, in culture the ex-type isolate of *Fusicolla epistroma* produces predominantly 3-septate conidia, rarely microconidia. From this, it remains unclear whether the associated anamorph on the type material of *N. magnusiana* is *Fusicolla epistroma*. Therefore, we decided to designate the epitype for *F. epistroma* based on Booth’s material and not to consider the older species name *Nectria magnusiana* for this species.

### Fusicolla matuo (Hosoya & Tubaki) Gräfenhan & Seifert, comb. nov. MycoBank MB519437.

**Basionym:** *Fusarium matuo* Hosoya & Tubaki, Mycoscience 45: 264. 2004.

≡ *Cosmospora matuo* Hosoya & Tubaki, Mycoscience 45: 262. 2004.

≡ *Fusarium splendens* Matuo & Takah. Kobay., nom. nud., Trans. Mycol. Soc. Japan 2(4): 13. 1960.

**Typification:** *Japan*. Honshu, Yamagata Pref., Mamuragawa-machi, Mogami-gun, on *Albizia julibrissin*, Oct. 1958, T. Kobayashi, holotype TNS F-11127, ex-type culture MAFF 410976.

**Other material examined:** Iran, Prov. Gilan, near Bandarepahlavi, on rotting stalk of Zea mays, Oct. 1968, D. Ershad, BBA 62154 = FRC E-0089 = NRRL 47180.

**Notes:** For a description, illustrations, and discussion of the telemorph and micro- and macroconidial synanamorphs of this species, see Hosoya & Tubaki (2004).

### Fusicolla merismoides (Corda) Gräfenhan, Seifert & Schroers, comb. nov. MycoBank MB519438.

**Basionym:** *Fusarium merismoides* Corda, Icon. Fung. 2: 4. 1838.

**Typification:** *Czech Republic*. Prague, on very wet shards of a plant pot, winter 1836, Corda, holotype PRM 155493.

**Notes:** *Fusicolla merismoides* is morphologically well characterised and has been widely accepted as a distinctive species (Wollenweber 1931, Booth 1971, Gerlach & Nirenberg 1982, Nelson and has been widely accepted as a distinctive species (Wollenweber 1931, Booth 1971, Gerlach & Nirenberg 1982, Nelson.

Unlike *F. beta*, which is mainly known from roots and tubers of plants, *F. merismoides* is commonly isolated from soils, polluted water, slime fluxes of trees, rotting plant material, and many other substrates. Gräfenhan et al. (2008) discovered several phylogenetic lineages in the *F. merismoides* morphological species, including some ascospore isolates; the same conclusion can be drawn from publicly available sequences attached to this name. We studied Corda’s type material deposited in PRM and could not come to a satisfying conclusion on the selection of an appropriate epitype based solely on the macroconidial characteristics. Moreover, after examination of authentic material of *Fusarium biasolettianum* (PRM 155487), we could not confirm the reported synonymy with *Fusicolla merismoides* (Wollenweber & Reinking 1935). Macroconidia of *Fusarium biasolettianum* have almost an pointed and slightly hooked apical cell and a pedicellate basal cell (Fig. 5) that rather resemble macroconidium characteristics of *Fusarium s. str*. species. Rossman et al. (1999) mentioned *Chrysoglaucum biasolettianum nom. rej.*, but there is no nomenclatural connection between this teleomorphic fungus and *F. biasolettianum*; the coincidental epithets indicate only that they were named in honour of the Italian botanist B. Biasolletto.

Most of the varieties within *F. merismoides* are distinct species, either within *Fusicolla* or in sister genera.

### Fusicolla violacea Gräfenhan & Seifert, sp. nov. MycoBank MB519439.

≡ *Fusarium merismoides var. violaceum* W. Gerlach, Phytopathol. Z. 90: 34. 1977. nom. inval. Art. 37.

**Latin description in Gerlach, Phytopath. Z. 90: 34-35. 1977 under the name “*Fusarium merismoides var. violaceum*”.**

**Typification:** *Iran*. Prov. Gilan, near Rasht, on Quadraspidiotus perniciosus (San José insect) scale on twig of *Prunus domestica*, Nov. 1968, W. Klett, holotype CBS 634.76, permanently cryopreserved culture, ex-type cultures BBA 62461 = NRRL 20896. GenBank barcodes: HQ897696 (rpb2).

**Notes:** For descriptions, illustrations, and discussion of the micro- and macroconidial synanamorphs of *F. violacea*, see Gerlach (1977) and Gerlach & Nirenberg (1982).

The taxon was not validly published because the author did not designate a holotype, instead listing one living strain with accession numbers in two culture collections as “Cultura tipica”.

### Macroconia (Wollenw.) Gräfenhan, Seifert & Schroers, gen. et stat. nov. MycoBank MB519441.

**Basionym:** *Nectria sect. Macroconia Wollenw.*, Angew. Bot. 8: 179. 1926. MycoBank MB519440.

**Type species:** *Nectria leptosphaeriae* Niessl in Krieger 1886, here recognised as *Macroconia leptosphaeriae* (Niessl) Gräfenhan & Schroers.

**Stroma** inconspicuous or absent. *Perithecia* solitary, subglobose with or without a small apical papilla, collapsing cupulate when dry, orange to carmine red, KOH+ dark red to violet, sometimes with hyphal hairs arising from outer wall, usually 100–250 μm high. *Asci* cylindrical to narrowly clavate, with a simple apex, 8 uniseriate to partially biseriate ascospores. *Ascospores* yellowish, 1-septate, smooth or becoming striate when mature. *Conidiophores* initially as lateral phialides on somatic hyphae, later monochasial to
verticillate, hyaline. *Phialides* monophialidic, cylindrical to subulate, hyaline. *Macroconidia* absent or very rare, when present ellipsoidal to allantoid, hyaline. *Macrosporium* robust, subcylindrical to moderately curved, apical cell conical or hooked, basal cell mostly conspicuously pedicellate, 3–7(–14)-septate, hyaline, mostly thick-walled. *Chlamydospores* absent or rare, when present globose, single, in pairs, or in chains in hyphae.

Colonies on PDA slow- or very slow-growing, 7–10 or ~45 mm diam in 14 d at room temperature, whitish to orange or reddish brown; aerial mycelium abundant, with discrete pink, orange or reddish brown sporodochia or small pinnnotes.

**Habitat:** Mostly growing on stromata of other ascomycetes on herbaceous plants or deciduous trees.

**Notes:** Based on the section name originally in *Nectria* (Wollenweber 1926), but also used as a “Gruppe” in *Fusarium* (Wollenweber & Reinking 1935), we raise *Macronia* to generic rank here for five species with large *Fusarium*-like macroconidia and minute perithecia.

**Accepted species**

*Macronia leptopsphaeriae* (Niessl) Gräfenhan & Schroers, **comb. nov.** MycoBank MB519442.

*Basionym:* *Nectria leptopsphaeriae* Niessl in Krieger, Fungi Saxonici Exsiccati. Die Pilze Sachsen’s 4: No. 165. 1886.

- *Cucurbitaria leptopsphaeriae* (Niessl) O. Kuntze, Rev. Gen. Plant. 3: 461. 1898.
- *Hypomyces leptopsphaeriae* (Niessl) Wollenw., Fus. autogr. del., Edn 1: No. 57. 1916.
- *Lasiocenchn leptopsphaeriae* (Niessl) Petch, Trans. Brit. Mycol. Soc. 21: 267. 1938.
- *Cosmospora leptopsphaeriae* (Niessl) Rossman & Samuels in Rosman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 122. 1999.

?= *Fusarium sphaeriae var. majus* Wollenw., *Fus. autogr. del. No. 859. 1930.

**Typification:** Germany. Sachsen, Königstein Fortress, church yard, on *Leptopsphaeria dolichon* on stems of *Urtica dioica*, Sept. & Oct. 1885, W. Krieger, Krieger's Fungi Saxonici 102. 1886.

*Notes:* For description, illustrations, and discussion of the teleomorph and macroconidial anamorph of this species, see Luo & Zhuang (2008). Its inclusion in *Macronia* is inferred from the morphology and sequences provided in the protologue, although we did not include the species in our own analysis.

*Macronia gigas* (J. Luo & W.Y. Zhuang) Gräfenhan & Seifert, **comb. nov.** MycoBank MB519444.

*Basionym:* *Cosmospora gigas* J. Luo & W.Y. Zhuang, Fungal Diversity 31: 85. 2008 non *Fusarium gigas* Speg., Anales Soc. Ci. Argent. 22: 221. 1866.

**Typification:** Taiwan. Nantou, Huisun Forestry Farm, 700 m alt., on rotten stem of bamboo associated with other fungi, Aug. 2005, W.Y. Zhuang 6598, holotype HMAS 95692, *ex-type* culture HMAS 173239; *paratype* ibid., W.Y. Zhuang, 6595, HMAS 97513. GenBank barcodes: EF121863 (*ITS*), EF121869 (28S rDNA).

*Notes:* For description, illustrations, and discussion of this teleomorph and macroconidial anamorph of this species, see Luo & Zhuang (2008). Its inclusion in *Macronia* is inferred from the morphology and sequences provided in the protologue, although we did not include the species in our own analysis.

*Macronia papilionacearum* (Seaver) Gräfenhan & Seifert, **comb. nov.** MycoBank MB519445.

*Basionym:* *Nectria papilionacearum* Seaver, Mycologia 1: 62. 1909.

≡ *Cosmospora papilionacearum* (Seaver) Rossman & Samuels in Rosman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 124. 1999.

?= *Fusarium gigas* Speg., *Anales Soc. Ci. Argent. 22: 221. 1866.

**Typification:** USA, Missouri, Lebanon, on living *Lespedeza* with *Parodieidia perliporionoides*, Jul. 1887, Kellerman 1003, lectotype NY designated by Samuels et al. 1991.

**Notes:** For a description, illustrations, and discussion of this teleomorph and macroconidial anamorph of this species, see Samuels et al. (1991). Our material collected in Florida closely resembles the description of *M. papilionacearum* given by Samuels et al. (1991), except for the smooth ascospores; the specimen from Florida has striate ascospores. In culture, the macroconidial anamorph of the Florida collection corresponded with the sketchy descriptions of *Fusarium gigas* (Wollenweber 1916, Wollenweber & Reinking 1935, Booth 1971, Gerlach & Nirenberg 1982). We found no anamorphic structures during our examination of the type material of *Fusarium gigas* (*Paraguay*, Arroyo-Guazu, on sterile pyrenomycete on culm of *Bambuseae*, Jan. 1882, B. Balansa, Pl. du Paraguay 3471, Specigazini’s Fungi Guaranitici 426, B 700014033, B 700014032, PAD). The synonymy of *M. papilionacearum* with the macroconidial anamorph
represented by the name "Fusarium" gigas should be confirmed using fresh South American material.

**Macroconia sphaeriae** (Fuckel) Gräfenhan & Schroers, *comb. nov.* MycoBank MB519446.

*Basionym: Fusarium sphaeriae* Fuckel, Jahrb. Nassausischen Vereins Naturk. 23–24: 370, 1870.

\[ ? = Nectria leptosphaeriae var. macrospora Wollenw. , Angew. Bot. 8: 187. 1926. \]

**Typification:** Germany. Hessen, Rheingau, Reichartsahrnau near Oestrich-Winkel, on Leptosphaeria (Sphaeria) dioica on Urtica dioica, in spring. L. Fuckel, Fuckel Fungi Rhenani 212, *lectotype* designated here G 00111017, *isotypes B, DAOM 126601 = Herb. Barby-Boissier 2034.

**Notes:** The macroconidial anamorph and the teleomorph of this species is described, illustrated, and discussed by Wollenweber (1916, No. 58; 1926). The proposed new combination moves an anamorphically typified epityp in a teleomorphically typified genus, resulting in a valid, legitimate but technically incorrect name under the present Art. 59.

*Macroconia sphaeriae* can be distinguished from *Leptosphaeria* by its larger ascospores and smaller conidia (Wollenweber 1926; see *M. leptosphaeriae* above). The lectotype material in G had a few ascomata, but the two perithecia studied contained neither asci nor ascospores. The isotype material lacked teleomorph structures. We follow Wollenweber’s (1926) conclusion and treat the two as separate species.

**Mariannaea** G. Arnaud ex Samson, Stud. Mycol. 6: 74, 1974.

**Type species:** *Mariannaea elegans* (Corda) Samson 1974.

**Strona** absent or inconspicuous. *Perithecia* solitary, globose with a flat apex, not collapsing or collapsing by lateral pinching when dry, pale yellow, orange or brown, KOH–, smooth or finely roughened, 250–350 μm high. *Asci* cylindrical to narrowly clavate, with a sometimes inconspicuous apical ring, 8 uniseriate or apically biseriate ascospores. *Ascospores* hyaline, 1-septate, smooth to spinulose when mature. *Conidiophores* verticillate to penicilliate, hyaline, with conidigenous cells arising directly from the stipe or from whorls of metulae on lower parts of the stipe, the stipe hyaline or yellowish brown at the base, often roughened at the base. *Phialides* monophialidic, flask shaped, hyaline, usually with obvious periclinal thickening and inconspicuous collarettes. *Conidia* aseptate, hyaline, in imbricate chains that eventually collapse to form slimy heads. *Chlamydospores* produced by some species.

**Notes:** *Mariannaea* is a common hyphomycete genus in soil and on woody substrates, and includes mononematous species with verticillate conidiophores, phialidic conidigenous cells, and often imbricate chains of aseptate conidia. The genus was validly published by Samson (1974) and his concept is accepted for this anamorph typified genus, with the addition of teleomorph characters above. Although the conidia are small, the conidiophores and conidia are not comparable to microconidia of the *Fusarium* complex, and the genus is included here because of the similarity of its teleomorph to the *Cosmospora* complex. In common with many of the teleomorph-anamorph connections discussed in this paper, the exact identities of the relevant morphs are imprecise. A teleomorph of a fungus similar to *M. elegans* was described from specimens collected in Jamaica and Venezuela as "Nectria" *mariannaea* by Samuels & Seifert (1991). Although it is Cosmospora-like, the name was not transferred by Rosman et al. (1999) and remains misclassified in *Nectria*. As discussed below, it seems unlikely that "N." *mariannaea* is the teleomorph of *M. elegans* s. str., and we are unable to infer its identity with any other of the named anamorphic species. An LSU sequence for the ex-type culture of *N. mariannaea* was deposited in GenBank (AY554242) by Schroers et al. (2005); the LSU of the ex-type of *M. samuelsii* (HQ843786) differs by 5 substitutions from *N. mariannaea*, and 3 substitutions from *M. aquatica*. Thus, given the limited amount of variation in the ITS and LSU normally seen in the *Nectriaceae*, the phylogenetic data suggest that *M. aquatica*, *N. mariannaea* and *M. samuelsii* represent different species. We elect not to describe a new genus for *N. mariannaea*, preferring to use the older *Mariannaea* as a holomorphic genus. Transferring it to *Mariannaea* would create a tautonym (Art. 23.4), thus, we have elected to leave this name in limbo until its taxonomic status can be more thoroughly evaluated.

Some of the species described in *Mariannaea* do not belong to the *Nectriaceae*, but to the *Cordycipitaceae* (Liang 1991, Liu et al. 2002). A phylogenetic analysis of internal transcribed spacer sequences of nectriaceous *Mariannaea* species was provided by Li et al. (2009) and suggests the existence of four species, including the type, *M. elegans*, a variety distinguished from the type that seems to be distinct at the species level, i.e. *M. aquatica*, *M. campylostroma*, and *M. elegans* var. *punicea*. To this we add a fifth species, *M. samuelsii* described below.

**Mariannaea samuelsii** Seifert & Bissett, *sp. nov.* MycoBank MB519447. Fig. 6.

Colonies in agar malo et pepeto confeito post 7 dies 21 mm diam, aureo-brunnea vel brunneo-aureatae; in agar farina aveae confeito 28–29 mm diam, sub luce auranto-griseae, obtusate griseo-aureae. *Conidiophores* 100–200 μm longa, stipite 2–3 μm lato, bis vel ter verticillata, verticillos terminales (2–)3–5 μlato, in verticillis subterminalibus 25–35 mm distanibus 1–3 phialides ferentia; raro phialides singulae circa 20 μm longae ex hyphis repentibus orientes. *Phialides* 12–30 mm longae, in parte latissima 2–3 μm latae, subulatae, in summo periclinali incrassatae, collari inconspicuo cincto praedecia. *Conidia* 3.5–7.5 × 2.5–3.5 μm, late fusiformia vel ellipsoidea, symetrica, sed saepe asymmetrica ex apertura conidiogenae protrusa, hyalina, levia, in calenis imbricatis saepe collabentibus adhaerentia. Holotypus DAOM 238914 (cultura dessicata).

On Blakeslee’s MEA: *Conidiophores* arising from the agar surface, from aerial hyphae or fascicles, mostly 100–200 μm long, the axis 2–3.5 μm wide, branching 2–3 level verticillate, with a terminal whorl of (2–)3–5 phialides, and 1–2 lower nodes of 1–3 phialides spaced 25–35 μm apart, sometimes with a basal branch that repeats the pattern of 1–2 levels of verticillate branching, rarely with phialides single and terminal on an intercalary cell about 20 μm long. *Phialides* 12–30 μm long, 2–3.5 μm wide at broadest part (19.8 +/- 0.9 × 2.9 +/- 0.06, n = 25), subulate, sometimes with base slightly swollen, often longest in basal whorls, periclinal thickening obvious with phase contrast, collarette inconspicuous, about 1 × 1 μm, cylindrical. *Conidia* 3.5–7.5 × 2.5–3.5 μm (6.0 +/- 0.2 × 3.1 +/- 0.06, n = 25), broadly fusiform or ellipsoidial, L/B ratio about 2–2.5, symmetrical but often sitting asymmetrically on conidiogenous aperture, hyaline, smooth-walled, in imbricate chains that quickly collapse into hyaline, slimy heads. *Chlamydospores* rarely produced, globose to ellipsoidial, hyaline, ~5–10 × 3–5 μm, in chains of up to five cells.

Colonies on Blakeslee’s MEA after 7 d about 21 mm diam, golden brown to brownish orange (5D6) in centre, fading towards entire margin, planar, with sparsely lanose aerial mycelium and fascicles, reverse concolourous; sporulation more intense on MEA in presence of 12:12 h fluorescent light:continuous darkness, agar surface mealy. On OA 28–29 mm diam, orange gray (5B2)
in light, and grayish orange (5D2) in dark, fading towards entire, thin margin, with moderately dense lanose aerial mycelium and fascicles, reverse concolourous.

Typification: Guatemala. Zacapa Prov., San Lorenzo Mt., isolated from soil under Podocarpus sp., surface litter and humus horizons, containing roots, 0–2 cm, 12 Jul. 1986, John Bissett, herb. DAOM 235814, ex-type culture CBS 125515. GenBank barcodes: HQ843766 (28S rDNA), HQ843767 (ITS), HQ897752 (rpb2), HQ897888 (acl1).

Notes: Mariannaea samuelsii is morphologically similar to M. elegans, the type of the genus (Samson 1974), and the recently described M. aquaticola (Li et al. 2009) in producing verticillate conidiophores and imbricate chains of fusiform conidia. The conidiophores of M. aquaticola and M. samuelsii are generally less elaborately branched than those of M. elegans, and lack basal roughening. The size ranges of the conidia of these three species overlap, with conidia of M. samuelsii (3.5–7.5 × 2.5–3.5 μm) intermediate in length between the shorter conidia of M. elegans (4–6 × 1.5–2.5 μm) and the longer conidia of M. aquaticola (5–10 × 2–4.5 μm). Mariannaea elegans produces chlamydospores, which have not been seen in M. aquaticola and are rarely and sparsely produced in M. samuelsii.

Mariannaea samuelsii differs by four base-pair substitutions (two in the ITS1, two in the ITS2) from M. aquaticola, its sister species.

Microcera Desm., Ann. Sci. Nat., Bot., sér. 3, 10: 359. 1848.
= Pseudomicrocera Petch, Trans. Brit. Mycol. Soc. 7: 164. 1921.

Type species: Microcera coccophila Desm. 1848.

Stroma and/or white byssus covering host. Perithecia solitary or in groups, globose, with a blunt papilla, collapsing cupulate or pinched when dry, orange to dark red, KOH+ dark red or violet, finely roughened, 200–400 μm high. Asci cylindrical to narrowly clavate, with an apical ring, 8 uniseriate ascospores. Ascospores hyaline to pale yellow-brown, 1(–3)-septate, smooth or becoming tuberculate when mature. Conidiophores initially as lateral phialides on somatic hyphae, later monochaial, verticillate to penicilliate, hyaline, usually forming discrete sporodochia or synnemata on the host. Phialides monophialidic, cylindrical to subulate to subclavate, hyaline. Microconidia absent. Macrococidial pale, orange, pink or bright red in mass, subcylindrical, moderately curved, or conspicuously curved, apical cell often slightly or conspicuously hooked, basal cell scarcely to conspicuously pedicellate, mostly (0–)3–5-septate, but up to 12 septate in one species, hyaline, mostly thick-walled. Chlamydospores not observed.

Colonies on PDA slow growing, 18–35 mm diam in 14 d at room temperature, surface smooth, felt-like or floccose, whitish to bright orange-red, sometimes with violet or vinaceous tones; aerial mycelium sparse or appressed, sporulation occurring in sporodochia or sometimes in slimy masses (pionnotes).

Habitat: Mostly parasites of scale insects, also reported on aphids, adelgids, and sometimes isolated as saprobes from soil or plant debris.

Notes: Along with Atractium discussed above, Microcera was a generic name used for synnematous Fusarium-like fungi, but in this case mostly parasites of scale insects. Our phylogenetic analysis confirms the significance of this ecological association, and the genus is here redefined to include additional non-synnematous species associated with scale insects, some of which are sometimes also found on other substrates. Until the 1920’s, the generic name Microcera was widely used for entomogenous species with slender, falcate conidia (McAlpine 1899, 1904; Parkin 1906; Trabut 1907; Miyabe & Sawada 1913; Petch 1921). The original concept of Microcera included one species, M. coccophila, based on two collections made by Roberge near Caen, France. Desmazières did not
mention perithecia on these specimens, but from the conidial shape he inferred a close relationship with *Fusarium*. Tulasne & Tulasne (1861, 1865) studied these and additional specimens from the type and other locations. They redescribed the species as a holomorph as *Sphaerostilbe flammea*, but concluded that Desmazières' *Microcera* was a "Silbum" with long, curved, *Fusarium*-like macroconidia. Petch (1921) revised this group of entomogenous species and studied the type material of *M. coccophila*, finding perithecia on well-developed stromata associated with the synnemata of the anamorph. Mature perithecia were red with ascospores measuring 12–18 × 5–7 μm (Petch 1921).

The taxonomic synonymy of *Microcera* with *Fusarium* followed the work of Wollenweber. Wollenweber (1916) first classified *F. ciliatum* in *Microcera*, based on his study of two herbarium specimens originally identified as *Fusarium pallens* (Wollenweber 1916: 1st edition, No. 435, 436). Later, Wollenweber & Reinking (1935) discarded *Microcera* and placed its species in *Fusarium*. In his first monographic revision of *Fusarium* Wollenweber (1931) did not consider *M. coccophila*, but subsequently revised his generic concept profoundly (Wollenweber & Reinking 1935). Then, *M. coccophila*, along with species described in other genera such as *Atractium*, *Discofusarium*, *Fusidium*, *Fusispornium*, *Fusoma*, *Microcera*, *Pionnotes*, *Pseudomicrocera*, and *Selenospornium* were placed in *Fusarium*. Of these, only the type species of *Pseudomicrocera* (Ps. *henningsii*) would now be considered a member of the *Microcera* clade. After Wollenweber's work, *Microcera* was included as a synonym in major revisions of *Fusarium*, e.g. Booth (1971), Gerlach & Nirenberg (1982), Nelson et al. (1983), and Leslie et al. (2006).

Twenty species were included in *Microcera* by various authors, and the present status of most species is known (Table 4). We presently accept four species, which can be keyed out as follows.

### KEY TO SPECIES OF MICROCERA

1. Macroconidia straight to slightly curved, up to 140 μm long, up to 12 septate ......................................................... *M. coccophila*
   1. Macroconidia distinctly curved, usually less than 120 μm long, mostly 3–5 septate ................................................................. 2

2. Macroconidia slender, 40–120 μm long ............................................................... *M. diploa*
   2. Macroconidia usually less than 40 μm long ............................................................... 3

3. Agar colonies with red pigments .................................................................................. *M. rubra*
   3. Agar colonies lacking red pigments ........................................................................... *M. larvarum*

**Accepted species**

*Microcera coccophila* Desm., Ann. Sci. Nat., Bot., Sér. 3, 10: 359. 1848. Fig. 7A, B.  
*Basionym:* *Tubercularia coccophila* (Desm.) Bonord., Abh. Geb. Mykol., p. 96. 1864.  
≡ *Fusarium coccophilum* (Desm.) Wollenw. & Reinking, Die Fusarien, p. 34. 1935.  
≡ *Fusarium episphaeria f. coccophilum* (Desm.) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 32: 662. 1945.  
≡ *Microcera pluriseptata* Cooke & Massee in Cooke, Grevillea 17: 43. 1888.  

**Typification**: France, Normandy, near Caen, on *Eulecanium tiliae* (nut scale) on living and young trunks of *Salix* and *Fraxinus* excelsior, Feb. 1847, M. Roberge, *lectotype* designated here K (M) 165807, Plants Cryptogames de France, Ed. II, Ser. I, No. 1350, *isotypes* P, K (M) 165806, Plants Cryptogames de France Ed. I, Ser. I, No. 1750.  

**Additional material examined**: Japan, Saitama, Hitani-gun, Ogawa-machi, on scale insect on *Broussonetia kazinoki* × *B. papyrifera*, Jul. 1993, G. Okada.

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**Table 4.** Species attributed to *Microcera* and their current status. Basic nomenclatural data from *Index Fungorum* (www.indexfungorum.org).

| Species, authority and year of publication | Status | Reference |
|------------------------------------------|--------|-----------|
| *M. acuminata* (Ellis & Everh.) Höhn. 1919 | = *Fusarium acuminatum* | Wollenweber & Reinking 1935 |
| *M. aurantiicola* Petch 1921 | = *M. larvarum* | This paper |
| *M. brachyospora* Sacc. & Scal. 1904 | = *Fusicolla aquaeductuum* | Wollenweber & Reinking 1935 |
| *M. ciliata* (Link) Wollenw. 1916 | = *"Fusarium” ciliatum, status unclear* | — |
| *M. clavariella* Speig. 1886 | = *Cladostigma fusispora* Pat. | Seifert 1985b |
| *M. coccidiphthora* Petch 1921 | = *Fusarium tasmanianum* (McAlpine) Rossman 1983 | Rossman 1983 |
| *M. coccophila* Desm. 1868 | Accepted species | This paper |
| *M. curta* Sacc. 1909 | = *M. larvarum* | This paper |
| *M. empmens* Ellis & Everh. 1894 | Unknown | — |
| *M. fujikuroi* Miyabe & Sawada 1913 | = *M. diploa* | This paper |
| *M. henningsii* (Koord.) Petch 1914 | = *M. diploa* | This paper |
| *M. massariiae* Sacc. 1886 | = *"Fusarium” ciliatum, see above* | Wollenweber & Reinking 1935 |
| *M. merrillii* Syd. 1914 | = *M. diploa* | This paper |
| *M. mytilus* McAlpine 1904 | = *Fusarium latentium var. longum* | Wollenweber & Reinking 1935 |
| *M. orthospora* Syd. 1924 | = *Mycogloea orthospora* (Syd.) R. McNabb ex Dingley 1989 | Dingley 1989 |
| *M. parlatoriae* Trab. 1907 | = *M. larvarum* | This paper |
| *M. plurisepatata* Cooke & Massee 1886 | = *M. coccophila* | This paper |
| *M. rectispora* Cooke & Massee | = *Tetricium rectisporum* (Cooke & Massee) Petch 1921 | Petch 1921 |
| *M. tasmanica* McAlpine 1904 | = *Fusarium tasmaniacum* (McAlpine) Rossman 1983 | Rossman 1983 |
| *M. tonduzi* Pat. 1912 | = *M. larvarum* | This paper |
Notes: The macroconidial anamorph and the teleomorph of this species as lectotypified here is described and discussed in detail by Petch (1921). For description, illustrations, and further taxonomic synonyms of the anamorph, see Gerlach & Nirenberg (1982).

There has been confusion about synonymies and anamorph-teleomorph connections between this fungus, *M. diploa*, and *M. larvarum*. Petch (1921) synonymised the anamorphic name *Atractium flammeum* Berk. & Ravenel with *Microcera coccophila*, arguing that *Sphaerostilbe flammea* Tul. & C. Tul. represented the holomorph of *M. coccophila* and that *Sphaerostilbe coccophila* Tul. & C. Tul. was actually a different species, *M. larvarum* (as "Nectria" auranticola). He cited two Desmazières exsiccati of *M. coccophila*, namely *Plantes Cryptogames de France*, Ed. I, Ser. I, No. 1750 and *ibid*. Ed. II, Ser. I, No. 1350. Our reexamination of the latter confirms Petch’s observation that mature perithecia have 1-septate ascospores, 12–18 × 5–7 μm, associated with the anamorph. "Nectria" flammea reportedly has larger ascospores (Dingley 1951, 15–24 × 6–10 μm; Booth 1971, 16–20 × 7.5–10 μm). The anamorph-teleomorph connection of *Microcera coccophila* with "Nectria" flammea needs to be critically reevaluated.

Gräfenhan et al. (2008) noted the occurrence of several phylogenetic species among anamorph and teleomorph collections that are morphologically similar to *M. coccophila*, *M. diploa*, and *M. larvarum*.

**Microcera diploa** (Berk. & M.A. Curtis) Gräfenhan & Seifert, *comb. nov.* MycoBank MB519448.

**Basionym:** *Nectria diploa* Berk. & M.A. Curtis, *J. Linn. Soc., Bot.* 10: 378. 1869.

≡ *Cucurbitis diploa* (Berk. & M.A. Curtis) O. Kuntze, *Rev. Gen. Plant.* 3: 461. 1898.
≡ *Crecneectria diploa* (Berk. & M.A. Curtis) Seaver, *Mycologia* 1: 190. 1909.
≡ *Caloneectria diploa* (Berk. & M.A. Curtis) Wollenw., *Angew. Bot.* 8: 193. 1926.
≡ *Cosmospora diploa* (Berk. & M.A. Curtis) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, *Stud. Mycol.* 42: 121. 1999.
≡ *Fusarium coccidicola* Hen. *as "coccideicola"*, *Bot. Jahrb. Syst.* 34: 57. 1904.
≡ *Aschersonia henningsii* Koord., *Bot. Untersuch. Java* p. 213. 1907.
≡ *Microcera henningsi* (Koord.) Petch, *Ann. Roy. Bot. Gard. Peradeniya* 5: 533. 1914.
≡ *Pseudomicrocera henningsi* (Koord.) Petch, *Trans. Brit. Mycol. Soc.* 7: 164. 1921.
≡ *Microcera fujikuroi* Miyabe & Sawada, *J. Coll. Agric. Tohoku Imp. Univ.* 5: 83. 1913.
≡ *Microcera merrilli* Syd., *Ann. Mycol.* 12: 576. 1914.

**Typification:** Cuba, on individual scale insects on bark, C. Wright 606 ex Herb. Berk., *Fungi Cubensis Wrightiana* 737, *lectotype* K designated by Booth 1971, *isotypes* FH 00286651, FH 00286652, NYS.

Notes: The holotype of this species is consistent with the descriptions of the teleomorph by Booth (1971) and Rossman (1983). The macroconidial anamorph is described by Booth (1971), Gerlach & Nirenberg (1982), and Rossman (1983). As explained in the introduction, under the present Art. 59, the proposed new combination results in a technically incorrect but valid and legitimate name.
Microcera diploa is an entomogenous species reported from many tropical and subtropical regions (Booth 1971, Rossman 1983), commonly found on various scale insects sitting on several plant species. Booth (1971) studied the type collection and reported pustules of perithecia on a stroma associated with the anamorph. From our observations of the same material, it is clear that the stromata developed over individual scale insects. In agreement with Rossman (1983), we follow Booth's decision to interpret the Cuban specimen as the type of Nectria diploa. Several Fusarium species were synonymised with M. diploa, namely F. derridis, F. juranum, and F. pentaclethrae, which were described only from herbaceous material (Wollenweber & Reinking 1935). We studied Hennings' material (F. derridis = B 700014017; F. juranum = B 700014035, B 700014036; F. pentaclethrae = B 700014037), and none seem to be insect-associated. Therefore, we reject these synonyms, except for F. coccidicola as listed above.

Microcera larvarum (Fuckel) Gräfenhan, Seifert & Schroers, comb. nov. MycoBank MB514499. Fig. 7C, D. Basionym: Fusarium larvarum Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 369. 1870. = Microcera parlatoriae Trab., Bull. Agric. Algérie Tunisie 13: 33. 1907. = Microcera curta Sacc., Ann. Mycol. 7: 437. 1909. = Microcera thonzii Pat., Bull. Soc. Mycol. France 28: 142. 1912. = Microcera auranthiicola Petch, Trans. Brit. Mycol. Soc. 7: 163. 1921.

Typification: Germany, Hessen, Rheingau, near Oestrich-Winkel, on larva cuticles of insects on apple trees, in spring. L. Fuckel, lectotype designated here G 00110115 Epitype designated here: Iran, Prov. Gilan, near Rasht, on Quadraspispidotus pericosmus (San José insect) scale on Prunus domestica, Oct. 1968, W. Gerlach & D. Ershad, epitype BBA, ex-type cultures BBA 62239 = CBS 738.79 = MUC1 19033 = NRRL 20473. GenBank barcodes: HQ897768 (rpb2), HQ897904 (act1).

Notes: For descriptions, illustrations, and further taxonomic synonyms of the teleomorph and macroconidial anamorph of this species, see Petch (1921), Wollenweber (1931), Booth (1971, 1981a, c), and Gerlach & Nirenberg (1982).

Our phylogenetic analysis and that of Bills et al. (2009) clearly indicate that the two varieties of M. larvarum segregated by Gerlach (1977) warrant species rank: M. larvarum var. rubrum is recognised as a distinct species below. Bills et al. (2009) studied pampafung production by species of this complex, and their data suggest that perhaps two additional phylogenetic species may exist in this group.

The synonymy of Microcera larvarum with "Nectria" auranthiicola cited by Booth (1971, 1981a), Gerlach & Nirenberg (1982), and Rossman et al. (1999) should be critically reviewed.

Microcera rubra Gräfenhan & Seifert, sp. nov. MycoBank MB514540. = Fusarium larvarum var. rubrum W. Gerlach, Phytopath. Z. 90: 38. 1977. nom. inval. Art. 37.

Latin description in Gerlach, Phytopath. Z. 90: 38. 1977 under the name "Fusarium" larvarum var. rubrum.

Typification: Iran, Prov. Gilan, near Rasht, on Quadraspispidotus pericosmus (San José insect) scale on Prunus domestica, Oct. 1968, W. Gerlach & D. Ershad, holotype CBS H-714, ex-type cultures BBA 62460 = CBS 638.76 = NRRL 20475 = NRRL 22111 = NRRL 22170. GenBank barcodes: HQ897767 (rpb2), HQ897903 (act1).

Notes: For descriptions, illustrations, and discussion of this macroconidial species, see Gerlach (1977) and Gerlach & Nirenberg (1982); for phylogenetic relationships, see Bills et al. (2009).

The taxon was not validly published because the author did not designate a holotype, instead listing one living strain with accession numbers in two culture collections as "Cultura typica".

Pseudonectria Seaver, Mycologia 1: 48. 1909.

Type species: Pseudonectria rousseliana (Mont.) Clements & Shear 1931, here recognised as P. buxi (DC.) Seifert, Gräfenhan & Schroers.

Notes: Pseudonectria as presently circumscribed is not monophyletic (Fig. 1), with two species branching out in separate clades in the Nectriaceae. The type species of Pseudonectria, together with an undescribed taxon, forms a sister clade to Atractum. The second species, "Pseudonectria" pachysandricola together with "Nectria" diminuta and "N." rubropeziza, falls between the terminal and basal Fusarium-like clade. Therefore, only one species is presently recognised in this genus, with the teleomorph typifying the oldest available generic name Pseudonectria 1909, and the anamorph representing the type of the later generic name Chaetodochium. There is presently no acceptable generic name for "Pseudonectria" pachysandricola, which is well described and illustrated by Dodge (1944) and Rossman et al. (1993).

The anamorphs of Pseudonectria are fairly well understood pathogens on the Buxaceae (Bezerra 1963, Rossman et al. 1993), but these species are usually cited under their anamorph names, i.e. "Volutella" buxi and "V." pachysandricola. Because these species do not share common morphological characters with Volutella s. str. (see below) and are phylogenetically distinct, these anamorph names should not be used. The phylogenetic relationship of a biologically and morphologically similar species described from Ruscus aculeatus, "V." ruscii, remains unresolved.

Pseudonectria buxi (DC.) Seifert, Gräfenhan & Schroers, comb. nov. MycoBank MB514541. Basionym: Tuberculatrix buxi DC., Flore française, Edn. 3 (Paris) 6: 110. 1815. = Chaetostroma buxi (DC.) Corda, Icon. Fung. 2: 30. 1838. = Volutella buxi (DC.) Berk., Outl. Brit. Fungi p. 340. 1860. = Chaetodochium buxi (DC.) Höhn., Mitt. bot. Inst. tech. Hochsch. Wien 9: 45. 1932. = Pseudonectria rousseliana (Mont.) Clements & Shear, Genera of Fungi p. 280. 1931. = Nectria rousseliana Mont. in Castagne, Cat. P1. Marseille Suppl. p. 44. 1851. For additional obligate synonyms, see Rossman et al. 1993.

Notes: Bezerra (1963) and Rossman et al. (1993) redescribed and illustrated both the anamorph and teleomorph of P. buxi, a common pathogen of Buxus sempervirens. The conidia of the anamorph tend toward fusiform, a shape not seen in species of Volutella s. str., and the sporodochia tend to be broadly attached to the substratum. These are subtle characters, and at present we cannot suggest robust morphological characters to unequivocally distinguish the anamorphs of Pseudonectria from Volutella. However, the teleomorphs are rather different, with the perithecia of Volutella being red and those of Pseudonectria being green.

Because this fungus has a known teleomorph and anamorph, Art. 59 applies, and our transfer of an anamorphically typified epithet to a teleomorphically typified generic name is technically incorrect according to the present ICBN, but it is valid and legitimate.

Stylonectria Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Wien, Math.-Naturwiss. Kl., Abt. 1, 124: 52. 1915.

Type species: Stylonectria applanata Höhn. 1915.

Stroma thin, whitish or yellow, hyphal or subiculum-like. Perithecia gregarious in groups of up to 20, subglobose, pyriform to comma-shaped; neck thin, whitish or yellow, hyphal or subiculum-like. Perithecia of the anamorph together with an undescribed taxon, forms a sister clade to Atractum. The second species, "Pseudonectria" pachysandricola together with "Nectria" diminuta and "N." rubropeziza, falls between the terminal and basal Fusarium-like clade. Therefore, only one species is presently recognised in this genus, with the teleomorph typifying the oldest available generic name Pseudonectria 1909, and the anamorph representing the type of the later generic name Chaetodochium. There is presently no acceptable generic name for "Pseudonectria" pachysandricola, which is well described and illustrated by Dodge (1944) and Rossman et al. (1993).

The anamorphs of Pseudonectria are fairly well understood pathogens on the Buxaceae (Bezerra 1963, Rossman et al. 1993), but these species are usually cited under their anamorph names, i.e. "Volutella" buxi and "V." pachysandricola. Because these species do not share common morphological characters with Volutella s. str. (see below) and are phylogenetically distinct, these anamorph names should not be used. The phylogenetic relationship of a biologically and morphologically similar species described from Ruscus aculeatus, "V." ruscii, remains unresolved.
subcylindrical, with a rounded or broad, circular, flat disc on a venter-like neck, sometimes laterally collapsing when dry, pale yellow, orange-red, orange-brown, or pale to dark red, KOH+ dark red to purple, yellow in lactic acid, smooth, usually shiny, slightly iridescent, 150–250(–350) μm high. Perithecial wall consisting of two regions: inner region of hyaline, thin-walled, compressed, elongate cells; outer region of distinct, isodiametric to oblong, angular or globose, thick-walled cells. Ascii cylindrical to clavate, apex simple or with a ring, with 8 uniseriate, biseriate or irregularly disposed ascospores. Ascospores hyaline or yellow to pale brown, 1-septate, cylindrical to allantoid or ellipsoidal, smooth or tuberculate, generally thick-walled.

**Ascomycota**

**Phialides** initially formed mostly as unbranched phialides on somatic hyphae, occasionally loosely branched, sometimes forming small sporodochia. **Phialides** monophialidic, almost cylindrical to subcylindrical, often with a distinct collarette. **Microconidia** sparsely produced, allantoid to lunulate, slightly to strongly curved, aseptate, subcylindrical, often with a distinct collarette. **Macroconidia** sparsely produced, allantoid to lunulate, slightly to strongly curved, aseptate, in slimy heads. **Macroconidia** orange in mass, subcylindrical or moderately to strongly curved, falcate, mostly 0–1-septate, apex narrower than base, apical cell blunt or hooked, basal cell not or scarcely pedicellate. **Chlamydospores** not observed.

In culture on PDA slow- to very slow-growing, 10–30 mm diam in 14 d at room temperature, surface white, later becoming off-white to pale or bright orange, occasionally with orange sporodochia; aerial mycelium mostly lacking, if present, sparse and appressed to pale or bright orange, occasionally with orange sporodochia; yellow in lactic acid, smooth, usually shiny, slightly iridescent, orange-red, orange-brown, or pale to dark red, KOH+ dark red to purple, yellow in lactic acid, smooth, usually shiny, slightly iridescent.

**Habitat:** Restricted to stromata of ascomycetes, mainly in the Diaporthales.

**Notes:** **Stylonectria** was described by Höhnel (1915) as an anamorph genus with the type and only species, *S. applanata*, for which the teleomorph was considered to be *Nectria* *applanata.* Booth (1959) presented convincing evidence that Höhnel’s type material of *Stylonectria* *applanata* (G 00111018) suggests *Nectria* and that of Fuckel’s *"Nectria" applanata* (G 00111019) suggests the two species are not conspecific, but both are species of *Stylonectria*; the latter is therefore renamed here.

The distribution of **Stylonectria carpini** corresponds to the distribution of *Carpinus betulus* in Europe. In North America, a different species of **Stylonectria** occurs on a black pyrenomycete on the congeneric native host, *Carpinus caroliniana,* and has a microconidial anamorph in culture and a distinctly different teleomorph. Collections made from a pyrenomycete on *Betula* are morphologically similar to *S. carpini* but phylogenetically distinct.

**Stylonectria purtonii** (Grev.) Gräfenhan, comb. nov. MycoBank MB519453. **Basionym:** *Cosmospora purtonii* (Grev.) Rossman & Samuels in *Rossman, et al. Mycol. Res. 108* (2004). **Notes:** This species produces both a micro- and a macroconidial synanamorph in addition to a teleomorph. Our examination of Höhnel’s type material of **Stylonectria* *applanata* *(FH 00286663)* and that of Fuckel’s *"Nectria"* *applanata* *(G 00111019)* suggests the two species are not conspecific, but both are species of *Stylonectria*; the latter is therefore renamed here.

The distribution of **Stylonectria carpini** corresponds to the distribution of *Carpinus betulus* in Europe. In North America, a different species of **Stylonectria** occurs on a black pyrenomycete on the congeneric native host, *Carpinus caroliniana,* and has a microconidial anamorph in culture and a distinctly different teleomorph. Collections made from a pyrenomycete on *Betula* are morphologically similar to *S. carpini* but phylogenetically distinct.
Typhlocyta synnematous species in this genus is discussed here.

Other material examined: Austria, Niederösterreich, Distr. Mödling, Comm. Hinterbrühl, Wassergrenze, Finsterer Ganger west of Gießbrühl, margin of a forest road, elev. 400 m, map grid 7863/3, on Hapalocystis bicaudata on corticated dead branches of Ulmus glabra attached to the living tree, May 2009, H. Voglmayr, WU 29855, culture CBS 125490.

Notes: This species produces microconidia and macroconidia in culture; the teleomorph was only found in nature. For a description, illustrations, and discussion of the species, see Weese (1916).

Volutella Tode 1790 : Fr. 1832. Fungi Mecklenb. Sel. 1: 28. 1790 : Syst. Mycol. 3: 458, 466 1832, nom. cons. [non Volutella Forsk. 1775 (Lauraceae)]

Type species: Volutella ciliata (Alb. & Schw. : Fr.) Fr. 1832, typus cons.

Perithecia nonstromatic, pyriform, collapsing by lateral pinching or not collapsing when dry, brownish orange to brownish red, yellow in 100 % lactic acid, darkest around papilla, hyphal hairs covering surface, hyaline, thick walled. Perithecial wall 15–25 um wide, with two intergrading layers of angular cells; cells next to centrum thin walled; cells of layer region thick walled. Asci narrowly clavate to broadly cylindrical, apex with or without refractive ring, eight-spored. Ascospores fusiform or biconic, equally or unequally 2-celled, smooth or finely roughed, hyaline, white in mass, obliquely uninucleate or partially biseriate near base, completely filling each ascus. Conidiophores aggregated into sporodochia or synnema, with an inconstipuous basal stroma; unbranched, hyaline setae around margin of conidioema. Synnemata, when produced, determinate, pale, composed of a stipe of parallel hyphae and a divergent capitulum of conidiophores giving rise to a slimy conidial mass; differentiated marginal hyphae absent. Conidiophore branching once or twice monochasial, 2-level verticillate, monoverticillate or irregularly biverticillate. Conidiogenous cells monopodial, hyaline, subulate, usually with conspicuous periclinal thickening. Conidial masses slimy, white, yellow, orange or pink. Conidia aseptate, hyaline, ellipsoidal, ovate or oblong. Chlamydospores produced in culture by some species. Verticillium-like synanamorh present in some species: Conidiophores hyaline, with 2 or more whorls of conidiogenous cells; phialides and conidia with similar characters to those described for the conidioema. Agar cultures growing relatively slowly, usually less than 30 mm diam in 14 d, with little aerial mycelium.

Notes: Volutella is a classical hyphomycete genus that has received little study, despite the common occurrence and broad distribution of its species. The genus is typified by V. ciliata, which has sporodochial conidioema with conspicuous hyaline, thick-walled, unbranched, spine-like setae, phialidic conidiogenous cells arising from more or less penicillately branched conidiophores, and ameroconidia accumulating in a profuse, colourful slime. Domsch et al. (2007) provided a general overview of the type and a few other soil-borne species of the genus. In anticipation of a more comprehensive revision of Volutella, the inclusion of one synnematosus species in this genus is discussed here.

Volutella s. str. should be restricted to the claude that includes the type species, V. ciliata, V. consors (referred to as V. minima by Domsch et al. 2007), and the synnematosus V. citrinella. The telemorphs associated with Volutella provide clues to its polyphyly. "Cosmospora" consors was reported as the telemorph of V. ciliata by Samuels (1977, as Nectria consors); the identity of the anamorph was later changed to V. minima by Domsch et al. (2007). This species differs from V. ciliata primarily by its cylindrical conidia. Volutella citrinella, considered at more length below, has a similar teleomorph, "Nectria" stilbellae. Neither teleomorph genus is appropriate, with Cosmospora now restricted to species with Acremonium-like anamorphs, discussed above, and Nectria is restricted to species with Tubercularia anamorphs (Hirooka et al. 2011). We have elected not to describe a new teleomorph genus for this clade, preferring to refer to these fungi by the oldest available generic name Volutella. As noted by Summerbell et al. (2011) in their discussion of Trichothecium, replacing a classic and well known generic name with a virtually unknown teleomorphically typified generic name would be taxonomically capricious. The other two holomorphic species with anamorphs attributed to Volutella are species presently classified in Pseudonectria (see above), which produce setose perithecia and aseptate ascospores, rather different than the smooth- or rough-walled perithecia and 1-septate ascospores of V. citrinella and V. consors.

The synnematous fungus V. citrinella was formerly known as Stilbella acciculosa (Seifert 1985a) but is more appropriately classified in Volutella. There have been scattered comments in the literature about synnematous species of Volutella, including the comment by Domsch et al. (2007) that some strains or species are "short stipitate". Thus, the inclusion of synnematous species only subtly alters the existing generic concept. Although there was scant mention of Volutella in the monograph of the synnematous genus Stilbella by Seifert (1985a), it was included in the key to Stilbella-like genera because of these observations by other authors.

Few of the approximately 120 described species of Volutella have been revised, and most species were seldom reported after their original descriptions. A preliminary survey of type specimens accessioned in K by Seifert (unpublished) suggests that many of the described species represent Colletotrichum, Sarcopodium, and other anamorphic genera. Comparatively few species that conform to the modern concept were uncovered. However, given the morphological variation we have seen in unidentified specimens and cultures, we suggest Volutella s. str. will ultimately include many more species.

Accepted species

Volutella ciliata (Alb. & Schwein.) Fr., Syst. Mycol. 3: 467. 1832.
Basionym: Tubercularia ciliata Alb. & Schwein., Consp. fung. p. 68. 1805.

Typhlocyta: We were unable to locate authentic material of T. ciliata; the sole specimen in the Schweinitz herbarium (PH) dates to a later publication (Schweinitz 1822). Because this name is formally conserved, careful attention must be paid to appropriate typification, and we chose not to propose a neotype or epitype here.

Volutella consors (Ellis & Everh.) Seifert, Gräfenhans & Schroe, comb. nov. MycoBank MB519455.
Basionym: Dialonectria consors Ellis & Everh., J. Mycol. 4(12): 122. 1888.

≡ Nectria consors (Ellis & Everh.) Seaver, Mycologia 1: 61. 1909.
≡ Nectriella consors (Ellis & Everh.) Sacc., Syll. fung. 9: 941. 1891.
≡ Cosmospora consors (Ellis & Everh.) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 119. 1999.
≡ Volutella cornata Ellis, Bull. Torrey Bot. Club 9: 20. 1892.
Volutella minima Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1, 118: 1543. 1909. Typification: USA: Louisiana, St. Martinsville, Sep. 1888, Langlois 1485. Holotype NY (examined by Samuels 1977).

Material examined: Volutella comata. USA, New Jersey, Newfield, on fallen petioles on Robinia, June 1881, Ellis North American Fungi no. 811. Isotypes DAOM, K.

Notes: Volutella consors predates the commonly used name for this morphological species, V. minima and the newly synonymised V. comata. As noted in the Introduction, the transfer of a teleomorph typified name into an anamorph genus creates a technically incorrect name that is nevertheless valid and legitimate. Several morphological variants of this species exist including specimens with reddish brown sporodochial tissues and white conidial masses as in the isotypes of V. comata or white stipes and bright yellow conidial masses as in several specimens from India in CBS-H and IMI 205174, as Stilbella sp. In addition, some living strains have Verticillium-like synnemorphs as noted but not illustrated by Matsushima (1975) and visible in the strain CBS 552.89. This is probably a species complex, and the synonymies with V. minima and V. comata should be reevaluated in future studies.

Volutella citrinella (Cooke & Massee) Seifert, comb. nov. MycoBank MB519456. Fig. 8.

Basionym: Stilbum citrinellum Cooke & Massee, Grevillea 16: 81. 1887.

= Stilbium aciculosum Ellis & Everhart, J. Mycol. 1: 153. 1885.
≡ Stilbella aciculosa (Ellis & Everhart) Seifert, Stud. Mycol. 27: 44. 1985
non Volutella aciculosa (Ellis & Harkn.) Sacc., Syll. fung. 4: 687. 1886.

Notes: The holomorph was described and illustrated by Samuels & Seifert (1991). Seifert (1985a) noted that the hyphae of the synnema stipes of this species sometimes become slightly thick-walled, and, if they diverge from the synnema, may appear somewhat seta-like. With the sister relationship of V. citrinella to V. ciliata revealed by the phylogenetic analysis, the taxonomic significance of this morphological observation becomes clear. Examination of three cultures of this fungus and reexamination of a slide of the holotype of Stilbum aciculosum revealed thickness of hyphae with nearly occluded lumina in all of them. These hyphae (Fig. 7F–H) are 1.5–3 μm wide with cell walls thickened up to 1 μm at the base, thinning towards the acute apex. They are common on specimens from nature. In culture, they are less frequent sometimes giving the synnemata a slightly hirsute appearance, but they generally do not penetrate into the capitulum.

In addition to the distributional records provided by Seifert (1985a), specimens have since been examined originating in Grenada, New Zealand, and South Africa.

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