

An overview of the taxonomy, phylogeny, and typification of nectriaceous fungi in *Cosmospora*, *Acremonium*, *Fusarium*, *Stilbella*, and *Volutella*

T. Gräfenhan^{1,4*}, H.-J. Schroers², H.I. Nirenberg³ and K.A. Seifert¹

¹Eastern Cereal and Oilseed Research Centre, Biodiversity (Mycology and Botany), 960 Carling Ave., Ottawa, Ontario, K1A 0C6, Canada; ²Agricultural Institute of Slovenia, 1000 Ljubljana, Slovenia; ³Julius-Kühn-Institute, Institute for Epidemiology and Pathogen Diagnostics, Königin-Luise-Str. 19, D-14195 Berlin, Germany; ⁴Current address: Grain Research Laboratory, Canadian Grain Commission, 1404-303 Main Street, Winnipeg, Manitoba, R3C 3G8, Canada

*Correspondence: tom.graefenhan@grainscanada.gc.ca

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 *Atractium*, which is removed from synonymy with *Fusarium* and epitypified for two macroconidial synnematosus 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. ullevolea*. 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. merismoides* species complex, with several former varieties raised to species rank. Originally a section of *Nectria*, *Macroconia* 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. samuelsii*. *Microcera* 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 *Stylonectria* each produce a teleomorph and micro- and macroconidial synanamorphs. The *Volutella* species sampled fall into three clades. *Pseudonectria* is accepted for a perithecial and sporodochial species that occurs on *Buxus*. *Volutella* s. str. also includes perithecial and/or sporodochial species and is revised to include a synnematosus 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, *Buxus*, codon model, holomorph concept, unitary nomenclature, synnematosus hyphomycetes.

Taxonomic novelties: **New genus:** *Macroconia* (Wollenw.) Gräfenhan, Seifert & Schroers. **New species:** *Dialonectria ullevolea* Seifert & Gräfenhan, *Fusicolla violacea* Gräfenhan & Seifert, *Mariannaea samuelsii* Seifert & Bissett, *Microcera rubra* Gräfenhan & Seifert. **New combinations:** *Atractium holubovae* (Seifert, S.J. Stanley & K.D. Hyde) Seifert, *Atractium crassum* (Wollenw.) Seifert & Gräfenhan, *Cosmospora arxii* (W. Gams) Gräfenhan & Schroers, *Cosmospora berkeleyana* (P. Karst.) Gräfenhan, Seifert & Schroers, *Cosmospora butyri* (J.F.H. Beyma) Gräfenhan, Seifert & Schroers, *Cosmospora cymosa* (W. Gams) Gräfenhan & Seifert, *Cosmospora khandalensis* (Thirum. & Sukapure) Gräfenhan & Seifert, *Cosmospora lavitskiae* (Zhdanova) Gräfenhan & Seifert, *Cosmospora viridescens* (C. Booth) Gräfenhan & Seifert, *Fusicolla acetileraea* (Tubaki, C. Booth & T. Harada) Gräfenhan & Seifert, *Fusicolla aquaeductuum* (Radlk. & Rabenh.) Gräfenhan, Seifert & Schroers, *Fusicolla epistroma* (Höhn.) Gräfenhan & Seifert, *Fusicolla matuoi* (Hosoya & Tubaki) Gräfenhan & Seifert, *Fusicolla merismoides* (Corda) Gräfenhan, Seifert & Schroers, *Macroconia cupularis* (J. Luo & W.Y. Zhuang) Gräfenhan & Seifert, *Macroconia gigas* (J. Luo & W.Y. Zhuang) Gräfenhan & Seifert, *Macroconia leptosphaeriae* (Niessl) Gräfenhan & Schroers, *Macroconia papilionacearum* (Seaver) Gräfenhan & Seifert, *Macroconia sphaeriae* (Fuckel) Gräfenhan & Schroers, *Microcera diploa* (Berk. & M.A. Curtis) Gräfenhan & Seifert, *Microcera larvarum* (Fuckel) Gräfenhan, Seifert & Schroers, *Pseudonectria buxi* (DC.) Seifert, Gräfenhan & Schroers, *Stylonectria purtonii* (Grev.) Gräfenhan, *Stylonectria wegeliniana* (Rehm) Gräfenhan, Voglmayr & Jaklitsch, *Volutella citrinella* (Ellis & Everh.) Seifert, *Volutella consors* (Ellis & Everh.) Seifert, Gräfenhan & Schroers. **New name:** *Stylonectria 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 polyphyletic 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 *et al.* 2009). The majority of described *Cosmospora* species have *Acremonium*-like or *Fusarium*-like anamorphs, but hyphomycetous anamorphs classified in *Chaetopsina*, *Cylindrocladiella*, *Gliocladiopsis*, *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 teleomorph 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 *Bionectriaceae*, *Nectriaceae*, and *Hypocreaceae*. Within the *Cosmospora* complex, for example, this rationale was used in the corresponding generic concepts for *Nectriadiella* (teleomorph), with *Cylindrocladiella* (anamorph) (Schoch *et al.* 2000), and *Chaetopsinectria* (teleomorph) with *Chaetopsina* (anamorph) (Luo & Zhuang 2010).

Booth's broad concept of *Nectria* dominated for 30 years; he recognised "groups" of species including the *Episphaeria* group (Booth 1959). This group, with additional species, was revised first as *Nectria* subgenus *Dialonectria* 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 cosmariospora*, not *Nectria coccinea*, which is a different fungus), which Saccardo (1883) 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* (*Xylariales*, 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 *Haematonectria*, with some species remaining in *Nectria sensu* Booth. Members of a seventh genus, *Neocosmospora*, fall into the *Fusarium solanilHaematonectria* clade (O'Donnell *et al.* 2008), but no *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 *Arachnites* 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 *Dialonectria*, *Fusicolla*, *Microcera*, and *Stylonectria* for species and varieties of the former *Fusarium* sections *Arachnites*, *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 redelimited 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 desmazieri*, 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 pleiomorphic 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 one 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 Kornerup & 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 (*rpb2*) 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. PCR products of the larger subunit of the ATP citrate lyase (*acl1*, Nowrousian *et al.* 2000) was amplified using the newly designed primers *acl1*-230up (5'-AGC CCG ATC AGC TCA TCA AG-3') and *acl1*-1220low (5'-CCT GGC AGC AAG ATC VAG GAA GT-3') 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 *rpb2* 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 *acl1* 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, 60 °C for 2 min. Contig sequences were assembled using Sequencher 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, *rpb2* region 5–7, *rpb2* region 7–11, and *acl1*. Intergenic spacer regions and introns of the *rpb2* and *acl1* 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 *rpb2* and *acl1* 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 (attachmentspertaxon = 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 $\omega_1 < \omega_2 < \omega_3$ (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 (attachmentspertaxon = 2) and 10 000 generations without improving the topology parameter.

Table 1. Taxa used in molecular phylogenetic analysis.

| Unitary names used in phylogenies | Teleomorph name (most recent) | Anamorph name (most recent) | Strain † | Other No. † | Collector/ Depositor | Country | Substratum | <i>rpb2</i> | <i>act1</i> | ITS | GenBank Accession No. ‡ | LSU |
|--|---|---|-------------|---------------------------------------|----------------------|-----------------|---|-------------|-------------|----------|-------------------------|-----|
| <i>Acremonium lichenicola</i> W. Gams | | <i>Acremonium lichenicola</i> W. Gams | CBS 425.66* | | K.W. Gams | Germany | <i>Betula</i> sp., old leaf | HQ897724 | HQ897861 | – | – | – |
| <i>Acremonium macroclavatum</i> Ts. Watan. | | <i>Acremonium macroclavatum</i> Ts. Watan. | CBS 123922* | MAFF 238162 | T. Watanabe | Japan | Soil | HQ897740 | HQ897876 | HQ897806 | – | – |
| <i>Acremonium tsugae</i> W. Gams | | <i>Acremonium tsugae</i> W. Gams | CBS 788.69* | | J.E. Bier | Canada | <i>Tsuga heterophylla</i> | HQ897728 | HQ897865 | – | – | – |
| " <i>Albonectria</i> " <i>albida</i> Guu & Y.M. Ju | <i>Albonectria albida</i> (Rossman) | <i>Albonectria albida</i> (Rossman) Guu & Y.M. Ju | BBA 67603* | ATCC 44543; BBA 65209; C.T.R. 71-110 | C. T. Rogerson | Jamaica | Bark of woody stem | HQ897738 | HQ897874 | HQ897804 | – | – |
| <i>Albonectria albosuccinea</i> Rossman & Samuels | <i>Albonectria albosuccinea</i> (Pat.) Rossman & Samuels | <i>Albonectria albosuccinea</i> (Pat.) Rossman & Samuels | BBA 64502* | ATCC 44544; C.T.R. 71-188; NRRL 20459 | C.T. Rogerson | Venezuela | Wood | HQ897699 | HQ897837 | HQ897788 | U34554 | – |
| <i>Albonectria rigidiuscula</i> (Berk. & Broome) Rossman & Samuels | <i>Albonectria rigidiuscula</i> (Berk. & Broome) Rossman & Samuels | <i>Fusarium decemcellulare</i> Brick | CBS 122570 | BPI 863840; G.J.S. 01-170 | G.J. Samuels | Cameroon | Bark | HQ897760 | HQ897896 | HQ897815 | – | – |
| " <i>Albonectria</i> " <i>verrucosa</i> (Pat.) Rossman & Samuels | <i>Albonectria verrucosa</i> (Pat.) Rossman & Samuels | <i>Fusarium merisimoides</i> var. <i>crassum</i> Wollenw. | CBS 102163 | ATCC 208923; BBA 64786; G.J.S. 84-426 | G.J. Samuels | Venezuela | Recently cut bamboo | HQ897784 | HQ897920 | – | – | – |
| <i>Atractium crassum</i> (Wollenw.) Seifert & Gräfenhan | | <i>Atractium crassum</i> Wollenw. | CBS 180.31* | NRRL 20894 | H.W. Wollenweber | Germany | Water tap | HQ897722 | HQ897859 | – | U88110 | – |
| <i>Atractium stibaster</i> Link | | <i>Stibella fusca</i> (Sacc.) Seifert | DAOM 215627 | | K.A. Seifert | Canada / Quebec | Cut stump | HQ897748 | HQ897864 | – | HQ843769 | – |
| <i>Chaetopsina penicillata</i> Samuels | <i>Chaetopsina penicillata</i> (Samuels) J. Luo & W.Y. Zhuang | <i>Chaetopsina penicillata</i> Samuels | CBS 608.92* | ATCC 56205; G.J.S. 77-21 | G.J. Samuels | New Zealand | <i>Beilschmiedia tawa</i> , bark | HQ897709 | HQ897847 | HQ897798 | – | – |
| <i>Cosmospora arxii</i> (W. Gams) Gräfenhan & Schroers | <i>Acremonium arxii</i> W. Gams | <i>Acremonium arxii</i> W. Gams | CBS 748.69* | | K.W. Gams | Germany | <i>Hypoxylon</i> sp. | HQ897725 | HQ897862 | – | – | – |
| <i>Cosmospora butyri</i> (J.F.H. Beyma) Gräfenhan, Seifert & Schroers | <i>Tilachlidium butyri</i> J.F.H. Beyma | <i>Tilachlidium butyri</i> J.F.H. Beyma | CBS 301.38* | MUCL 9950 | Knudson | Denmark | Butter | HQ897729 | HQ897866 | – | – | – |
| <i>Cosmospora coccinea</i> Rabenh. | <i>Cosmospora coccinea</i> Rabenh. | <i>Verticillium olivaceum</i> W. Gams | CBS 341.70 | | K.W. Gams | Germany | Hymenium of <i>Inonotus nodulosus</i> on <i>Fagus sylvatica</i> | HQ897777 | HQ897913 | HQ897827 | – | – |
| <i>Cosmospora cymosa</i> (W. Gams) Gräfenhan & Seifert | <i>Acremonium cymosum</i> W. Gams | <i>Acremonium cymosum</i> W. Gams | CBS 762.69* | | K.W. Gams | Germany | <i>Inonotus radiatus</i> , decaying fruiting body | HQ897778 | HQ897914 | HQ897828 | – | – |
| <i>Cosmospora khandalensis</i> (Thinum. & Sukapure) Gräfenhan & Seifert | <i>Cephalosporium khandalense</i> Thinum. & Sukapure | <i>Cephalosporium khandalense</i> Thinum. & Sukapure | CBS 356.65* | ATCC 16091; IMI 112790; MUCL 7974 | M.J. Thirumalachar | India | <i>Bambusa</i> sp., decaying stem | HQ897723 | HQ897860 | – | – | – |
| <i>Cosmospora lavitskiae</i> (Zhdanova) Gräfenhan & Seifert | <i>Gliomastix lavitskiae</i> Zhdanova | <i>Gliomastix lavitskiae</i> Zhdanova | CBS 530.68* | ATCC 18666; IMI 133984 | L.A. Bejakova | Ukraine | Plant debris on surface soil | HQ897726 | HQ897863 | – | – | – |
| " <i>Cosmospora</i> " <i>stegonsporii</i> Rossman, D.F. Farr & Akulov | <i>Cosmospora stegonsporii</i> Rossman, D.F. Farr & Akulov | <i>Cosmospora stegonsporii</i> Rossman, D.F. Farr & Akulov | CBS 122305* | A.R. 4385; BPI 878274 | A.Y. Akulov | Ukraine | <i>Stegonsporium pyriforme</i> on bark | HQ897733 | HQ897869 | – | – | – |
| <i>Cosmospora</i> cf. <i>viridescens</i> (C. Booth) Gräfenhan & Seifert | <i>Nectria</i> cf. <i>viridescens</i> C. Booth | <i>Nectria</i> cf. <i>viridescens</i> C. Booth | CBS 102433 | | M. Reblova | Czech Republic | <i>Tilia</i> sp., dead tree | HQ897712 | HQ897850 | – | – | – |

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. ‡ | LSU |
|---|---|--|-------------|---|------------------------------|-----------------------------|--|-------------------------|-------------------|
| | | | | | | | | <i>act1</i> | ITS |
| <i>Cosmospora</i> sp. | | | CBS 213.70 | | K.W. Gams | Poland | <i>Fomitopsis pinicola</i> | HQ897864 | – |
| <i>Cyanonectria buxi</i> (Fueke) G. Schroers, Gräfenhan & Seifert | <i>Gibberella buxi</i> (Fueke) G. Winter | <i>Fusarium buxicola</i> Sacc. | BBA 64985 | | M.E. Noordeloos | Netherlands | <i>Buxus sempervirens</i> | HQ897882 | HQ897809 |
| <i>Cyanonectria cyanostoma</i> (Sacc. & Flageolet) Samuels & Chaverri | <i>Cyanonectria cyanostoma</i> (Sacc. & Flageolet) Samuels & Chaverri | | BBA 70964* | BPI 748307; CBS 101734; G.J.S 98-127 | G.J. Samuels & F. Candoussau | France | <i>Buxus sempervirens</i> , bark | HQ897895 | HQ897814 FJ474076 |
| <i>Cylindroccladium</i> sp. | | | CBS 125514 | K.A.S. 1732 | K.A. Seifert | New Zealand | Soil under <i>Leptospermum scoparium</i> | HQ897871 | HQ897801 |
| <i>Cylindrodendrum</i> sp. | | | DAOM 226786 | K.A.S. 872 | K.A. Seifert | Australia / New South Wales | Rotten wood | HQ897866 | – |
| <i>Dialonectria cf. episphaeria</i> (Tode : Fr.) Cooke | <i>Cosmospora cf. episphaeria</i> (Tode : Fr.) Rossmann & Samuels | | CBS 125494 | DAOM 235830; T.G. 2006-11 | T. Gräfenhan | Canada / Ontario | Old ascomycete stromata on deciduous tree | HQ897892 | HQ897811 |
| <i>Dialonectria ulivolea</i> Seifert & Gräfenhan | | <i>Fusarium aqueductum</i> var. <i>medium</i> Wollenw. | CBS 125493 | DAOM 235827; T.G. 2007-56 | T. Gräfenhan | USA / Pennsylvania | Ascomycete on <i>Fagus americana</i> | HQ897918 | – |
| " <i>Fusarium</i> " <i>cavispermum</i> Corda | | <i>Fusarium cavispermum</i> Corda | BBA 64137 | CBS 184.77; NRRL 20837; NRRL 22279 | T. Nilsson | Sweden | Untreated pine pole | HQ897898 | – |
| " <i>Fusarium</i> " <i>ciliatum</i> (Alb. & Schw.) Link | | <i>Fusarium ciliatum</i> (Alb. & Schw.) Link | BBA 62172 | ATCC 16068; ATCC 24137; CBS 191.65; CBS H-12687, IMI 112499; NRRL 20431 | H. Richter | Germany | On <i>Fagus sylvatica</i> | HQ897900 | HQ897818 AF228349 |
| " <i>Fusarium</i> " <i>dimerum</i> Penz. | | <i>Fusarium dimerum</i> Penz. | CBS 254.50 | NRRL 36384 | Mack | Netherlands | Man, sputum | – | EU926279 |
| " <i>Fusarium</i> " <i>domesticum</i> (Fr.) Bachm. | | <i>Fusarium domesticum</i> (Fr.) Bachm. | CBS 116517 | NRRL 29976 | K. O'Donnell | Switzerland | Cheese | – | EU926219 |
| <i>Fusarium graminearum</i> Schwabe | <i>Gibberella zeae</i> (Schwein.) Petch | <i>Fusarium graminearum</i> Schwabe | NRRL 31084 | PH-1 | | USA / Michigan | <i>Zea mays</i> | FGSG02659 ^o | – |
| " <i>Fusarium</i> " <i>lunatum</i> (Ellis & Everh.) Arx | | <i>Fusarium lunatum</i> (Ellis & Everh.) Arx | BBA 63199 | CBS 632.76; NRRL 20690; NRRL 37067 | W. Gerlach | Germany | <i>Gymnocalcium damsii</i> | HQ897902 | HQ897819 |
| " <i>Fusarium</i> " <i>melanochlorum</i> (Casp.) Sacc. | | <i>Fusarium melanochlorum</i> (Casp.) Sacc. | CBS 202.65 | ATCC 16069; B 700014030; BBA 62248; NRRL 36353 | H. Richter | Austria | Branch canker on <i>Fagus sylvatica</i> | HQ897905 | – |
| " <i>Fusarium</i> " <i>merismoides</i> var. <i>chlamydosporale</i> Wollenw. | | <i>Fusarium merismoides</i> var. <i>chlamydosporale</i> Wollenw. | CBS 179.31* | NRRL 20839 | H.W. Wollenweber | USA / Wisconsin | <i>Ostrya virginiana</i> | – | U88109 |
| " <i>Fusarium</i> " <i>nematophilum</i> Nirenberg & G. Hagedorn | | <i>Fusarium nematophilum</i> Nirenberg & G. Hagedorn | BBA 70838 | | A. Westphal | USA / California | <i>Beta vulgaris</i> / <i>Heterodera schachtii</i> | HQ897834 | HQ897786 |

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. ‡ | ITS | LSU |
|--|---|--|-------------|--|----------------------------|------------------|--|-------------------------|-------------|-------------------|
| | | | | | | | | <i>rbp2</i> | <i>act1</i> | |
| <i>Fusarium sambucinum</i> Fuckel | <i>Gibberella pulicaris</i> (Fr.) Sacc. | <i>Fusarium sambucinum</i> Fuckel | BBA 70569 | | H.I. Nirenberg | Germany | <i>Humulus lupulus</i> | HQ897751 | HQ897887 | – |
| <i>Fusarium subulnatum</i> Reinking | | <i>Fusarium subulnatum</i> Reinking | BBA 62431* | CBS 189.34; NRRL 13384; NRRL 20840 | O.A. Reinking | Costa Rica | Soil of banana plantation | HQ897780 | HQ897916 | HQ897830 |
| <i>Fusarium verticillioides</i> (Sacc.) Nirenberg | <i>Gibberella moniliformis</i> Wineland | <i>Fusarium verticillioides</i> (Sacc.) Nirenberg | NRRL 20956 | FGSC 7600; FRC M-3125 | | USA / California | <i>Zea mays</i> | FVEG09286° | FVEG04667° | – |
| " <i>Fusarium</i> " sp. | | | DAOM 235648 | BBA 62195; CBS 119875; K.A.S. 2872; MRC 1652 | R. Schneider | Germany | <i>Solanum lycopersicum</i> | HQ897698 | HQ897836 | HQ897787 |
| <i>Fusicolla acellirea</i> (Tubaki, C. Booth & T. Harada) Gräfenhan & Seifert | | <i>Fusarium merismoides</i> var. <i>acellireum</i> Tubaki, C. Booth & T. Harada | BBA 63789* | IMI 181488; NRRL 20827 | Miyoshi | Japan | Polluted soil | HQ897701 | HQ897839 | HQ897790 U88108 |
| <i>Fusicolla aquaeductuum</i> (Radlk. & Rabenh.) Gräfenhan, Seifert & Schroers | | <i>Fusarium</i> var. <i>aquaeductuum</i> var. <i>aquaeductuum</i> (Radlk. & Rabenh.) Lagerh. | BBA 63669 | CBS 734.79; NRRL 20686 | W. Gerlach | Germany | Drinking water | HQ897742 | HQ897878 | – |
| <i>Fusicolla betae</i> (Desm.) Bonord. | | <i>Fusarium betae</i> (Desm.) Sacc. | BBA 64317* | | C. Bauers | Germany | On young plants of <i>Triticum aestivum</i> | HQ897781 | HQ897917 | – |
| <i>Fusicolla epistroma</i> (Höhn.) Gräfenhan & Seifert | | <i>Fusarium epistroma</i> (Höhn.) C. Booth | BBA 62201* | IMI 85601; NRRL 20439 | W.G. Bramley | UK | Ascomycete on <i>Betula</i> sp. | HQ897765 | HQ897901 | AF228352 |
| <i>Fusicolla matuoi</i> (Hosoya & Tubaki) Gräfenhan & Seifert | <i>Cosmospora matuoi</i> Hosoya & Tubaki | <i>Fusarium matuoi</i> Hosoya & Tubaki | CBS 581.78 | ATCC 18694; MAFF 238445; NRRL 20427 | T. Matsuo | Japan | <i>Albizia julibrissin</i> | HQ897720 | HQ897858 | – |
| <i>Fusicolla violacea</i> Gräfenhan & Seifert | | <i>Fusarium merismoides</i> var. <i>violaceum</i> W. Gerlach, nom. inval. | CBS 634.76* | BBA 62461; NRRL 20896 | D. Ershad | Iran | <i>Quadrastiphiotus pernicius</i> on living on branch of <i>Prunus domestica</i> | HQ897696 | – | U88112 |
| <i>Geejeyessia atrofusca</i> (Schw.) Schroers & Gräfenhan | <i>Nectria atrofusca</i> (Schwein.) Ellis & Everh. | <i>Fusarium staphyleae</i> Samuels & Rogerson | CBS 125482 | DAOM 238118; T.G. 2006-01 | T. Gräfenhan | Canada / Ontario | <i>Staphylea trifolia</i> , twigs | HQ897775 | HQ897911 | HQ897825 |
| <i>Geejeyessia cellitridicola</i> Gräfenhan & Schroers | | | CBS 125481 | DAOM 238129; T.G. 2006-29 | T. Gräfenhan | Canada / Ontario | <i>Celtis occidentalis</i> , twigs | HQ897772 | HQ897908 | HQ897822 |
| <i>Geejeyessia cicatricum</i> (Berk.) Schroers | <i>Nectria cicatricum</i> (Berk.) Tul. & C. Tul. | | CBS 125550 | CBS H-20375; H.J.S. 1374 | H.-J. Schroers & M. Željav | Slovenia | <i>Buxus sempervirens</i> , twigs | HQ897697 | HQ897835 | – |
| <i>Geejeyessia desmazieri</i> (Becc. & De Not.) Schroers, Gräfenhan & Seifert | <i>Nectria desmazieri</i> Becc. & De Not. | <i>Fusarium fuckelii</i> Sacc. | CBS 313.34 | NRRL 20474 | E.W. Mason | UK | <i>Buxus sempervirens</i> , dead twig | HQ897703 | HQ897841 | HQ897792 U88125 |
| <i>Geejeyessia zealandica</i> (Cooke) Schroers | <i>Cosmospora zealandica</i> (Cooke) Samuels & Nirenberg | <i>Fusarium zealandicum</i> Nirenberg & Samuels | BBA 65034 | BPI 802575; CBS 101913; G.J.S. 86-509 | G.J. Samuels | New Zealand | <i>Plegianthus</i> , timber | HQ897745 | HQ897881 | HQ897808 |
| <i>Haematonectria illudens</i> (Berk.) Samuels & Nirenberg | <i>Haematonectria illudens</i> (Berk.) Samuels & Nirenberg | <i>Fusarium illudens</i> C. Booth | BBA 67606 | G.J.S. 82-98; NRRL 22090 | G.J. Samuels | New Zealand | <i>Beilschmiedia tawa</i> | HQ897692 | HQ897833 | AF178393 AF178362 |
| <i>Haematonectria ipomoeae</i> (Halst.) Samuels & Nirenberg | <i>Haematonectria ipomoeae</i> (Halst.) Samuels & Nirenberg | <i>Fusarium striatum</i> Sherb. | BBA 64379 | NRRL 22147 | H.I. Nirenberg | Germany | <i>Passiflora edulis</i> | HQ897753 | HQ897889 | – |

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. ‡ | ITS | LSU |
|---|---|--|--------------|--|----------------------|----------------------|---|-------------------------|----------|----------|
| | | | | | | | | <i>acI1</i> | | |
| <i>Heliscus lugdunensis</i> Sacc. & Thery | <i>Nectria lugdunensis</i> J. Webster | <i>Heliscus lugdunensis</i> Sacc. & Thery | CBS 125485 | DAOM 235831; T.G. 2008-07 | T. Gräfenhan | USA / Arizona | <i>Populus fremontii</i> , twigs in stream | HQ897867 | – | – |
| <i>Heliscus submersus</i> H.J. Huds. | | <i>Heliscus submersus</i> H.J. Huds. | CBS 394.62* | | H.J. Hudson | UK | | HQ897845 | HQ897796 | – |
| <i>Macroconia leptosphaeriae</i> (Niessl) Gräfenhan & Schroers | <i>Cosmospora leptosphaeriae</i> (Niessl) Rossmann & Samuels | ? <i>Fusarium sphaeriae</i> var. <i>majus</i> Wollenw. | CBS 100001 | CBS H-6030 | L. Rommelaars | Netherlands | On <i>Leptosphaeria</i> on dead stem of <i>Urtica dioica</i> | HQ897891 | HQ897810 | – |
| <i>Macroconia papilionacearum</i> (Seaver) Gräfenhan & Seifert | <i>Cosmospora papilionacearum</i> (Seaver) Rossmann & Samuels | ? <i>Fusarium gigas</i> Speg. | CBS 125495 | DAOM 238119; T.G. 2007-03 | T. Gräfenhan | USA / Florida | Black ascomycete on <i>Fabaceae</i> | HQ897776 | HQ897826 | – |
| <i>Macroconia</i> sp. | | | CBS 125496 | T.G. 2008-08 | T. Gräfenhan | USA / Arizona | <i>Quercus</i> sp., branch in stream of water | HQ897868 | – | – |
| <i>Mariannaea elegans</i> (Corda) Samson | ? <i>Nectria mariannaeae</i> Samuels & Seifert | <i>Mariannaea elegans</i> (Corda) Samson | DAOM 226709 | K.A.S. 948 | K.A. Seifert | Canada / Ontario | <i>Betula</i> sp., wood | HQ897747 | – | HQ843768 |
| <i>Mariannaea samuelisii</i> Seifert & Bissett | | | DAOM 235814* | CBS 125515; K.A.S. 1307 | J. Bissett | Guatemala | Soil under <i>Podocarpus</i> | HQ897752 | HQ843767 | HQ843766 |
| <i>Microcera coccophila</i> Desm. | | <i>Fusarium coccophilum</i> (Desm.) Wollenw. & Reinking | CBS 310.34 | NRRL 13962 | H.W. Wollenweber | Italy | Scale insect on <i>Laurus nobilis</i> | HQ897843 | HQ897794 | – |
| <i>Microcera diploa</i> (Berk. & M.A. Curtis) Gräfenhan & Seifert | <i>Cosmospora diploa</i> (Berk. & M.A. Curtis) Rossmann & Samuels | <i>Fusarium coccicola</i> Henn. | BBA 62173 | CBS 735.79; NRRL 13966 | W. Gerlach | Iran | <i>Quadrastipitiolus pernicius</i> on living on branch of <i>Prunus domestica</i> | HQ897763 | HQ897817 | – |
| <i>Microcera lanvarum</i> (Fueckel) Gräfenhan, Seifert & Schroers | | <i>Fusarium lanvarum</i> Fueckel | CBS 169.30 | NRRL 22102 | H.W. Wollenweber | Japan | Aphids on <i>Pyrus communis</i> | HQ897717 | – | – |
| <i>Microcera rubra</i> Gräfenhan & Seifert | | <i>Fusarium lanvarum</i> var. <i>rubrum</i> W. Gerlach, <i>nom. inval.</i> | BBA 62460* | CBS 638.76; NRRL 20475; NRRL 22111; NRRL 22170 | W. Gerlach | Iran | <i>Quadrastipitiolus pernicius</i> on living on branch of <i>Prunus domestica</i> | HQ897767 | HQ897820 | – |
| <i>Nalanthamala diospyri</i> (Crand.) Schroers & M.J. Wingfield | | <i>Nalanthamala diospyri</i> (Crand.) Schroers & M.J. Wingfield | CBS 429.89 | ATCC 22206 | B.S. Crandall | USA / Mississippi | <i>Diospyros virginiana</i> | HQ897718 | – | – |
| " <i>Nectria</i> " <i>cinereopapillata</i> Henn. & E. Nyman | <i>Nectria cinereopapillata</i> Henn. & E. Nyman | | CBS 264.36 | | H.W. Wollenweber | Sierra Leone | <i>Cassia sieberiana</i> | HQ897710 | HQ897799 | – |
| " <i>Nectria</i> " <i>diminuta</i> Berk. | <i>Cosmospora diminuta</i> (Berk.) Rossmann & Samuels | | CBS 114636 | BPI 864173; G.J.S. 00-181 | G.J. Samuels | USA / North Carolina | <i>Quercus virginiana</i> , dead tree | HQ897758 | HQ897813 | – |
| " <i>Nectria</i> " cf. <i>flavoviridis</i> (Fueckel) Wollenw. | <i>Nectria flavoviridis</i> (Fueckel) Wollenw. | | BBA 65542 | | G.J. Samuels | USA / New York | On fungus on decorticated wood | HQ897702 | HQ897791 | – |
| " <i>Nectria</i> " <i>magnoliae</i> M.L. Lohman & Hepting | <i>Nectria magnoliae</i> M.L. Lohman & Hepting | | CBS 380.50* | BPI 552527 | G.H. Hepting | USA / North Carolina | <i>Liriodendron tulipifera</i> | HQ897713 | – | – |
| <i>Nectria millina</i> (Mont.) Mont. | <i>Nectria millina</i> (Mont.) Mont. | | CBS 125499 | T.G. 2008-02 | T. Gräfenhan | USA / Arizona | <i>Yucca elata</i> | HQ897730 | – | – |
| <i>Nectria nigrescens</i> Cooke | <i>Nectria nigrescens</i> Cooke | | CBS 125500 | DAOM 235832; T.G. 2006-18 | T. Gräfenhan | Canada / Ontario | <i>Acer</i> sp., twig | HQ897757 | HQ897812 | – |
| <i>Nectria pseudotrichia</i> Berk. & M.A. Curtis | <i>Nectria pseudotrichia</i> Berk. & M.A. Curtis | <i>Tubercularia lateritia</i> (Berk.) Seifert | DAOM 235820 | T.G. 2007-41 | T. Gräfenhan | USA / Florida | Dead herbaceous plant | HQ897706 | HQ897844 | HQ897795 |

Table 1. (Continued).

| Unitary names used in phylogenies | Teleomorph name (most recent) | Anamorph name (most recent) | Strain † | Other No. † | Collector/ Depositor | Country | Substratum | <i>rpb2</i> | GenBank Accession No. † | ITS | LSU |
|--|---|--|-------------|---|----------------------|---------------------------|--|-------------|-------------------------|----------|----------|
| " <i>Nectria</i> " <i>risibethii</i> C. Booth | <i>Cosmospora risibethii</i> (C. Booth) Rossmann & Samuels | | CBS 496.67* | IMI 070248b; MUCL 4133 | J. Rishbeth | UK | <i>Pinus sylvestris</i> , stump | HQ897714 | HQ897862 | – | – |
| " <i>Nectria</i> " <i>rubropeziza</i> Wollenw. | <i>Nectria rubropeziza</i> Wollenw. | | CBS 234.31* | | H.W. Wollenweber | USA / Maryland | Tree trunk | HQ897708 | HQ897846 | HQ897797 | – |
| " <i>Nectria</i> " <i>setofusariae</i> Samuels & Nirenberg | <i>Nectria setofusariae</i> Samuels & Nirenberg | <i>Fusarium setosum</i> Nirenberg & Samuels | CBS 635.92 | A.R. 3333; BBA 65063; BPI 1113176; G.J.S. 88-12 | A.Y. Rossmann | French Guiana | Bark of recently cut tree | HQ897704 | HQ897842 | HQ897793 | – |
| " <i>Nectria</i> " <i>ventricosa</i> C. Booth | <i>Nectria ventricosa</i> C. Booth | <i>Fusarium ventricosum</i> Appel & Wollenw. | BBA 62452 | CBS 748.79; NRR 20846; NRR 22113 | K.H. Domsch | Germany | Wheat field soil | HQ897761 | HQ897897 | HQ897816 | L36613 |
| " <i>Nectria</i> " <i>ventricosa</i> C. Booth | <i>Nectria ventricosa</i> C. Booth | <i>Fusarium ventricosum</i> Appel & Wollenw. | CBS 430.91 | NRR 25729 | U. Kuchenbäcker | Germany | <i>Robinia pseudoacacia</i> , twig | HQ897771 | HQ897907 | – | – |
| <i>Nectria</i> sp. | | | CBS 125498 | T.G. 2006-33 | T. Gräfenhan | Canada / Ontario | <i>Abies balsamea</i> | HQ897737 | HQ897873 | HQ897803 | – |
| <i>Neocosmospora vasinfecta</i> E.F. Sm. | <i>Neocosmospora vasinfecta</i> E.F. Sm. | <i>Cylindrocarpon candidum</i> (Link) Wollenw. | NRR 22166 | ATCC 62199 | L.M. Carris | USA / Illinois | <i>Heterodera glycines</i> | EU329497 | – | DQ094319 | DQ236361 |
| <i>Neonectria coccinea</i> (Pers.) Rossmann & Samuels | <i>Neonectria coccinea</i> (Pers.) Rossmann & Samuels | <i>Cylindrocarpon candidum</i> (Link) Wollenw. | CBS 125484 | DAOM 235835; T.G. 2007-17 | T. Gräfenhan | Germany | <i>Fagus sylvatica</i> | HQ897785 | HQ897921 | HQ897832 | – |
| <i>Neonectria ditissima</i> (Tul. & C. Tul.) Samuels & Rossmann | <i>Neonectria ditissima</i> (Tul. & C. Tul.) Samuels & Rossmann | <i>Cylindrocarpon heteronema</i> (Berk. & Broome) Wollenw. | CBS 125486 | DAOM 235836; T.G. 2006-21 | T. Gräfenhan | Canada / Ontario | <i>Fagus americana</i> , branch | HQ897774 | HQ897910 | HQ897824 | – |
| <i>Neonectria fuckeliana</i> (C. Booth) Castl. & Rossmann | <i>Neonectria fuckeliana</i> (C. Booth) Castl. & Rossmann | | CBS 239.29* | IMI 039700 | H.W. Wollenweber | UK | <i>Picea sitchensis</i> , bark | HQ897711 | HQ897849 | – | – |
| <i>Pseudonectria buxi</i> (DC.) Gräfenhan & Schroers | <i>Pseudonectria rousseliana</i> (Mont.) Wollenw. | <i>Volutella buxi</i> (DC.) Berk. | CBS 125483 | T.G. 2007-69A | K.W. Gams | Spain | <i>Buxus sempervirens</i> , leaves | HQ897719 | HQ897857 | HQ897800 | – |
| " <i>Pseudonectria</i> " <i>pachysandricola</i> B.O. Dodge | <i>Pseudonectria pachysandricola</i> B.O. Dodge | <i>Volutella pachysandricola</i> B.O. Dodge | DAOM 195309 | | E.J. Mathers | USA / Florida | <i>Pachysandra</i> sp., nursery stock | HQ897743 | HQ897879 | HQ897807 | – |
| <i>Pseudonectria</i> sp. | | | BBA 71336 | | H.I. Nirenberg | Germany | <i>Buxus sempervirens</i> , leaves | HQ897741 | HQ897877 | – | – |
| <i>Stylonectria</i> cf. <i>applanata</i> Höhn. | <i>Nectria applanata</i> var. <i>succinea</i> Höhn. | | CBS 125489 | T.G. 2008-24 | T. Gräfenhan | Canada / Ontario | Ascomycete on <i>Betula</i> sp. | HQ897739 | HQ897875 | HQ897805 | – |
| <i>Stylonectria carpini</i> Gräfenhan | <i>Nectria applanata</i> Fuekel | | DAOM 235819 | W.J. 3013 | H. Voglmayr | Austria | On <i>Melanconis spodiacea</i> on <i>Carpinus betulus</i> | HQ897773 | HQ897909 | HQ897823 | – |
| <i>Stylonectria purtonii</i> (Grev.) Gräfenhan | <i>Cosmospora purtonii</i> (Grev.) Rossmann & Samuels | | DAOM 235818 | T.G. 2007-30 | T. Gräfenhan | Germany | On small branches of <i>Picea abies</i> | HQ897783 | HQ897919 | HQ897831 | – |
| <i>Stylonectria wegeliniana</i> (Rehm) Gräfenhan, Voglmayr & Jaklitsch | <i>Cosmospora wegeliniana</i> (Rehm) Rossmann & Samuels | | CBS 125490 | WU 29855 | H. Voglmayr | Austria | Stromata of <i>Hapalycystis bicaudata</i> on <i>Ulmus glabra</i> | HQ897754 | HQ897890 | – | – |
| <i>Stylonectria</i> sp. | | | CBS 125491 | T.G. 2007-21 | T. Gräfenhan | Germany | Ascomycete on <i>Carpinus / Ulmus</i> ? | HQ897779 | HQ897915 | HQ897829 | – |
| <i>Thebonectria discophora</i> (Mont.) P. Chaverri & C. Salgado | <i>Neonectria discophora</i> (Mont.) Mantiri & Samuels | <i>Cylindrocarpon ianthothele</i> var. <i>majus</i> Wollenw. | CBS 125487 | DAOM 235837; T.G. 2007-34 | T. Gräfenhan | Germany | <i>Aesculus hippocastanum</i> | HQ897700 | HQ897838 | HQ897789 | – |
| <i>Thebonectria lucida</i> (C. Booth) P. Chaverri & C. Salgado | <i>Cylindrocarpon lucidum</i> C. Booth | | DAOM 226723 | K.A.S. 1007 | K.A. Seifert | Canada / British Columbia | <i>Pseudotsuga menziesii</i> , root | HQ897734 | HQ897870 | – | – |

Table 1. (Continued).

| Unitary names used in phylogenies | Teleomorph name (most recent) | Anamorph name (most recent) | Strain † | Other No. † | Collector/ Depositor | Country | Substratum | <i>rpb2</i> | <i>ac1</i> | ITS | LSU |
|--|--|---|-------------|---------------|-----------------------------|---------------------------|---|-------------|------------|----------|----------|
| <i>Voluella ciliata</i> (Alb. & Schwein.) Fr. | | <i>Voluella ciliata</i> (Alb. & Schwein.) Fr. | DAOM 226718 | K.A.S. 972 | J.A. Traquir | Canada / Ontario | Agricultural soil | HQ897736 | HQ897872 | HQ897802 | – |
| <i>Voluella citrinella</i> (Cooke & Masseur) Seifert | <i>Cosmospora stilbellae</i> (Samuels & Seifert) Rossman & Samuels | <i>Stilbella aciculosa</i> (Ellis & Everh.) Seifert | DAOM 226720 | K.A.S. 978 | R.J. Bandoni & A.A. Bandoni | Canada / British Columbia | <i>Solanum tuberosum</i> , debris | HQ897770 | HQ897906 | HQ897821 | HQ843771 |
| <i>Voluella consors</i> (Ellis & Everh.) Seifert, Gräfenhan & Schroers | <i>Cosmospora consors</i> (Ellis & Everh.) Rossman & Samuels | <i>Voluella minima</i> Höhn. | CBS 328.77 | C.T.R. 72-347 | C.T. Rogerson | USA / North Carolina | <i>Magnolia fraseri</i> , old inflorescence | HQ897716 | HQ897854 | – | – |
| <i>Voluella consors</i> (Ellis & Everh.) Seifert, Gräfenhan & Schroers | <i>Cosmospora consors</i> (Ellis & Everh.) Rossman & Samuels | <i>Voluella minima</i> Höhn. | CBS 139.79 | | G.H. Boerema | Netherlands | Decaying orchid bulb | HQ897715 | HQ897853 | – | – |

† — Type or other authentic material.

‡ — GenBank accession numbers beginning with HQ were newly generated. All other sequences were obtained from GenBank.

° — Locus number in the *Fusarium* genome database (<http://www.broad.mit.edu/annotation/fungifusarium>)

† — A.R. = Amy Y. Rossman personal collection; ATCC = American Type Culture Collections, Manassas, Virginia, USA; B = Mycological Herbarium at the Botanical Museum, Berlin, Germany; BBA = Julius Kühn-Institute, Institute for Epidemiology and Pathogen Diagnostics, Berlin & Braunschweig, Germany; BPI = U.S. National Fungus Collections, USDA, ARS, Beltsville, Maryland, USA; CBS = Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; C.T.R. = Clark T. Rogerson personal collection; DAOM = Canadian National Mycological Herbarium and Culture Collection, AAFC, Ottawa, Ontario, Canada; FGSC = Fungal Genetics Stock Center, School of Biological Sciences, University of Missouri, Kansas City, Missouri, USA; FRC = Fusarium Research Center, Department of Plant Pathology, Penn State University, University Park, Pennsylvania, USA; G.J.S. = Gary J. Samuels personal collection; H.J.S. = Hans-Josef Schroers personal collection; IMI = CABI Bioservices, Egham, Surrey, UK; K.A.S. = Keith A. Seifert personal collection; MAFF = Microbial Culture Collection, National Institute of Agrobiological Sciences, Tsukuba, Japan; MRC = Microbial Culture Collection, South African Medical Research Council, Tygerberg, South Africa; MUCL = (Agro)Industrial Fungi & Yeasts Collection, Université Catholique de Louvain, Louvain-la-Neuve, Belgium; NRRL = ARS Culture Collection, USDA, NCAUR, Peoria, Illinois, USA; T.G. = Tom Gräfenhan personal collection; W.J. = Walter Jaklitsch personal collection; WU = Herbarium, Department of Plant Systematics and Evolution, Faculty of Life Sciences, University Vienna, Austria.

Non-parametric bootstrapping of 1 000 ML pseudo-replicates 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/ac1* 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 (Swofford 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 *ac1* 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

acl1 with 206 parsimony-informative characters) resulted in a single best ML tree with $-\ln L = -57,309.9782$ (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 = 0.2885, G = 0.2691, T = 0.2326; substitution rates AC = 2.104, AG = 6.386, AT = 2.011, CG = 0.767, CT = 9.725, GT = 1.000; proportion of invariable sites I = 0.3861; gamma distribution shape parameter $\alpha = 0.8858$. The parameters for the GTR + I + G model of the *rpb2* 7–11 partition were as follows: Estimated base frequencies; A = 0.2033, C = 0.3050, G = 0.2538, T = 0.2379; substitution rates AC = 1.680, AG = 7.167, AT = 2.089, CG = 0.914, CT = 10.966, GT = 1.000; proportion of invariable sites I = 0.5253; gamma distribution shape parameter $\alpha = 0.8815$. The parameters for the GTR + I + G model of the *acl1* partition were as follows: Estimated base frequencies; A = 0.1774, C = 0.3655, G = 0.2369, T = 0.2202; substitution rates AC = 0.982, AG = 2.844, AT = 0.638, CG = 0.839, CT = 7.876, GT = 1.000; proportion of invariable sites I = 0.4834; gamma distribution shape parameter $\alpha = 0.9192$.

Ten independent ML analyses under the codon substitution model (M3 with $K = 3$) of the combined and partitioned data set (*rpb2* 5–7 with 294 parsimony-informative characters, *rpb2* 7–11 with 292 parsimony-informative characters, and *acl1* with 145 parsimony-informative characters) resulted in a single best ML tree with $-\ln L = -54,991.4885$ (Fig. 1). 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 nonsynonymous rate categories $\omega_1 = 0.0020$ with $p_1 = 0.6471$, $\omega_2 = 0.0726$ with $p_2 = 0.2452$, $\omega_3 = 0.3214$ with $p_3 = 0.1077$. The parameters for the M3 codon model of the *rpb2* 7–11 partition were as follows: 61 empirical codon frequencies (F3×4 method); substitution rates AC = 1.023, AG = 2.820, AT = 1.177, CG = 0.933, CT = 2.489, GT = 1.000; and three estimated non-synonymous rate categories $\omega_1 = 0.0020$ with $p_1 = 0.8918$, $\omega_2 = 0.0925$ with $p_2 = 0.0985$, $\omega_3 = 0.5436$ with $p_3 = 0.0097$. The parameters for the M3 codon model of the *acl1* 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 $\omega_1 = 0.0031$ with $p_1 = 0.8025$, $\omega_2 = 0.1007$ with $p_2 = 0.1211$, $\omega_3 = 0.4420$ with $p_3 = 0.0763$. These dN/dS ratios ($\omega < 1$) verify a significant departure from neutrality ($\omega \approx 1$) of the *rpb2* and *acl1* data partitions implying natural selection against changes of amino acids in the encoding genes studied.

In comparison, the best ML tree for the M3 codon model received a significantly better negative-log likelihood score than the best ML tree under the GTR + I + G nucleotide substitution model. The topology of the phylograms did not differ for the clades studied. Only some basal lineages such as "*Nectria*" *diminuta*, "*N.*" *rubropeziza*, and "*Pseudonectria*" *pachysandricola* grouped differently using different substitution models, probably a result of long branch attraction.

Similarly, heuristic searches of the parsimony analysis yielded a single most parsimonious tree (not shown), which did not have a significantly different topology than that of the ML analyses. The MP tree was 14 023 steps with a consistency index (CI) of 0.152, a retention index (RI) of 0.492, a rescaled CI (RC) of 0.075, and a homoplasy index (HI) of 0.848.

1 000 ML pseudoreplicates, two independent MCMC analyses, and 1 000 heuristic bootstrap replicates of the combined and partitioned data set conducted with GARLI, MrBayes and PAUP, respectively, yielded majority consensus trees with highly

concordant topologies (not shown) similar to that of 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 $\geq 75\%$, Bayesian posterior probabilities (PP) is ≥ 0.95 , and MP bootstrap proportions (MP-BP) is $\geq 75\%$ (Lutzoni *et al.* 2004).

Polyphyly of *Cosmospora sensu* Rossman

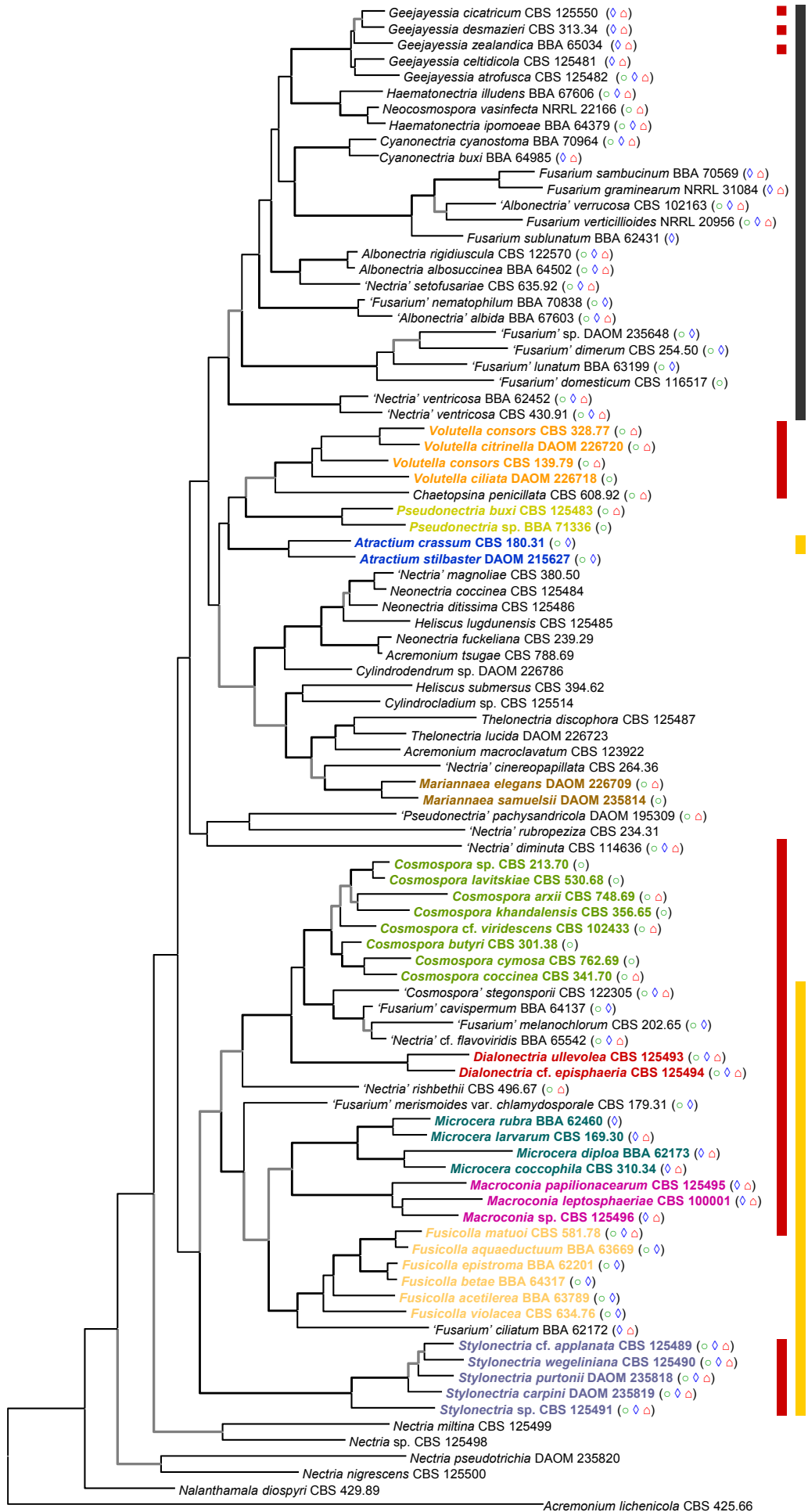
In the best ML tree (Fig. 1), species formerly placed in *Cosmospora sensu* Rossman fall into several major clades. The first major clade includes *Volutella* with four strains of three species, *V. ciliata*, *V. citrinella* ("*Cosmospora*" *stilbellae*) and *V. consors* ("*C.*" *consors*), in a strongly supported clade. *Chaetopsina penicillata* (= *Chaetopsinectria* or "*Cosmospora*" *chaetopsinae-penicillatae*) is a well supported sister species of *Volutella*, confirming the close phylogenetic 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*, *Cylindrodendrum*, *Heliscus*, *Mariannaea*, and *Neonectria*.

The second major clade includes species formerly classified as *Nectria applanata*, *Cosmospora purtonii*, and *C. wegeliniana*. This clade is strongly supported and comprises species having ascomata 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*, *Dialonectria*, *Fusicolla*, *Macroconia*, and *Microcera* below. *Cosmospora coccinea* forms a strongly supported clade with other well-known species of the genus with *Acremonium*-like anamorphs, such as *C. butyri*, *C. cymosa*, and *C. viridescens*. 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 *Dialonectria* clade, which contains *D. episphaeria* and a new species, *D. ullevolea*. 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.*" *cavispermum*, "*F.*" *ciliatum*, "*F.*" *melanochlorum*, and "*F.*" *merismoides* var. *chlamydosporale*, 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* + *acl1* gene sequence data set. Negative-log likelihood ($-\ln L$) 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 bold and grey. Symbols following strain numbers indicate different morphs known for the species: \circ = microconidial state, \diamond = *Fusarium*-like macroconidial state, \triangle = teleomorph. Vertical bars in red indicate members of *Cosmospora sensu* Rossman *et al.* (1999), yellow bars taxa of the basal *Fusarium*-like clade, and a dark grey bar species of the terminal *Fusarium* clade, respectively.



0.1

The terminal clade includes "*Nectria*" *desmazieri* and "*N.*" *atrofusca*, 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. subglutinatum*, 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 *Albonectria*, *Cyanonectria*, *Gibberella*, *Haematonectria*, 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 *Albonectria* and the *Haematonectria*/*Neocosmospora* species complex as well as the species pair "*Albonectria*" *albida* and "*Fusarium*" *nematophilum* always formed strongly supported groups.

The basal *Fusarium*-like clade, with numerous members formerly classified in *Fusarium* sections *Arachnites*, *Eupionnotes*, *Macroconia*, *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 stilbaster*, it forms a strongly supported sister lineage to a group of fungi including species of *Chaetopsina*, *Pseudonectria*, and *Volutella*.

Polyphyly of *Volutella sensu lato*

As mentioned above, *Volutella* and *Chaetopsina* form a well supported lineage that is distinct from *Cosmospora s. str.* and the basal *Fusarium*-like clade. The type of the genus *Pseudonectria*, *P. buxi*, together with another similar species (BBA 71336), form a strongly supported sister group to the *Volutella*/*Chaetopsina* lineage. *Chaetopsina* separates *Pseudonectria* from species of *Volutella s. str.* In contrast to the above-mentioned clades, "*Pseudonectria*" *pachysandricola* and "*Nectria*" *rubropeziza* 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.*" *pachysandricola* is only distantly related to the type species of *Pseudonectria* 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 *Cylindrocarpon* clade including the teleomorph genera *Ilyonectria*, *Neonectria*, *Rugonectria*, and *Thelonectria*, and the anamorph genus *Campylocarpon* (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 *Cylindrodendrum*, *Heliscus*, and *Mariannaea* 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, *acl1*, 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 analysis 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, *Cylindrocarpon*,

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 |
|---|---|--|--|---|
| <i>Fusisporium</i> Link 1809 | <i>F. aurantiacum</i> Link 1809 : Fr. | Wollenweber (1916) | <i>F. graminum</i> Corda or <i>F. sporotrichioides</i> Sherb. | = <i>Fusarium</i> , Gams & Nirenberg 1989 |
| <i>Atractium</i> Link 1809 | <i>A. stilbaster</i> Link 1809 | Wollenweber & Reinking (1935) | <i>A. stilbaster</i> Link | Distinct genus in <i>Nectriaceae</i> , this paper |
| <i>Selenosporium</i> Corda 1837 | <i>S. tubercularioides</i> Corda 1837 ≡ <i>Fusarium tubercularioides</i> (Corda) Sacc. 1886 | Lindau (1910), Wollenweber & Reinking (1935) | <i>F. avenaceum</i> (Corda) Sacc. or <i>F. lateritium</i> Nees | = <i>Fusarium</i> , Holubová-Jechová <i>et al.</i> 1994 |
| <i>Microcera</i> Desm. 1848 | <i>M. coccophila</i> Desm. 1848 | Wollenweber & Reinking (1935) | <i>M. coccophila</i> Desm. | Distinct genus in <i>Nectriaceae</i> , this paper |
| <i>Pionnotes</i> Fr. 1849 | <i>P. capitata</i> (Schw.) Fr. 1849 ≡ <i>Fusarium capitatum</i> Schw. 1832 | Wollenweber & Reinking (1935) | <i>Dacrymyces</i> sp. (PH!) | = <i>Dacrymyces</i> , Seifert <i>et al.</i> in prep. |
| <i>Fusicolla</i> Bonord. 1851 | <i>F. betae</i> (Desm. : Fr.) Bonord. 1851 ≡ <i>Fusisporium betae</i> Desm. 1830 : Fr. | Wollenweber (1916), Wollenweber & Reinking (1935) | <i>Fusicolla betae</i> (Desm.) Bonord. | Distinct genus in <i>Nectriaceae</i> , this paper |
| <i>Sporotrichella</i> P. Karst. 1887 | <i>S. rosea</i> P. Karst. 1887 | Wollenweber & Reinking (1935) | <i>F. sporotrichioides</i> Sherb. | = <i>Fusarium</i> |
| <i>Lachnidium</i> Giard 1891 | <i>L. acridiorum</i> Giard 1891 | Saccardo (1901), Wollenweber & Reinking (1935) | <i>F. solani</i> complex | = <i>Fusarium</i> |
| <i>Discocolla</i> Prill. & Delacr. 1894 | <i>D. pirina</i> Prill. & Delacr. 1894 | Wollenweber & Reinking (1935) | <i>F. lactis</i> Pirota & Riboni | = <i>Fusarium</i> |
| <i>Septorella</i> Allesch. 1897 | <i>S. salaciae</i> Allesch. 1897 | Höhnel (1912) | Unknown | Status uncertain |
| <i>Trichofusarium</i> Bubák 1906 | <i>T. rusci</i> Bubák 1906 ≡ <i>Fusarium roseum</i> var. <i>rusci</i> Sacc. 1886 | Wollenweber & Reinking (1935), Sutton (1986) | <i>Pycnofusarium rusci</i> D. Hawksw. & Punith. | Considered distinct by Schroers (pers. comm.) |
| <i>Ustilaginoidella</i> Essed 1911 | <i>U. musaepeda</i> Essed 1911 | Brandes (1919) | <i>F. oxysporum</i> complex | = <i>Fusarium</i> |
| <i>Stagonostroma</i> Died. 1914 | <i>S. dulcamarae</i> (Pass.) Died. 1914 ≡ <i>Stagonospora dulcamarae</i> Pass. 1890 | Sutton (1977) | Unknown | Status uncertain |
| <i>Fusariopsis</i> Horta 1919 | <i>F. derrienii</i> Horta 1919 | Dodge (1935) | Unknown | Unknown |
| <i>Discofusarium</i> Petch 1921 | <i>D. tasmaniense</i> (McAlpine) Petch 1921 ≡ <i>Microcera tasmanica</i> McAlpine 1904 ≡ <i>Fusarium tasmanicum</i> (McAlpine) Rossman 1983 | Rossmann (1983) | " <i>Fusarium</i> " anamorph of " <i>Nectria</i> " <i>coccidophaga</i> (Petch) Rossman 1983 | Unknown |
| <i>Pseudomicrocera</i> Petch 1921 | <i>P. henningsii</i> (Koord.) Petch 1921 ≡ <i>Aschersonia henningsii</i> Koord. 1907 | Wollenweber & Reinking (1935) | <i>Microcera diploa</i> | = <i>Microcera</i> , this paper |
| <i>Fusidomus</i> Grove 1929 | Not designated | Sutton (1977) | Unknown | Status uncertain |
| <i>Infracungus</i> Cif. 1951 | <i>I. micropus</i> (Sacc.) Cif. 1951 ≡ <i>Fusarium micropus</i> Sacc. 1921 | Wollenweber & Reinking (1935) | <i>Fusarium lateritium</i> complex | = <i>Fusarium</i> |
| <i>Euricoa</i> Bat. & H. Maia 1955 | <i>E. dominguesii</i> Bat. & H. Maia 1955 | Summerbell & Schroers (2002) | <i>F. solani</i> complex | |
| <i>Hyaloflorea</i> Bat. & H. Maia 1955 | <i>H. ramosa</i> Bat. & H. Maia 1955 | W. Gams (pers. comm.) | <i>F. solani</i> complex | = <i>Fusarium</i> |
| <i>Pseudofusarium</i> Matsush. 1971 | <i>P. fusarioideum</i> Matsush. 1971 = <i>Pseudofusarium semitectum</i> (Berk. & Rav.) Matsush. 1975 | Pascoe (1990) | <i>F. semitectum</i> auct. | <i>Fusarium</i> , Matsushima 1980 |
| <i>Pycnofusarium</i> Punith. 1973 | <i>P. rusci</i> D. Hawksw. & Punith. 1973 | Sutton (1986) | <i>Pycnofusarium rusci</i> D. Hawksw. & Punith. | = <i>Trichofusarium</i> , 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 *Chaetopsina* 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 megaconidia 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 perithecial 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, usually on scale insects. 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. merismoides* 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 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* monophialidic, hyaline, subulate, with conspicuous periclinal thickening. Conidial masses yellow to orange. *Conidia* (0–)1–5-septate, clavate, obovoid 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. Stroma elongatum, capitatum. Sporidia fusiformia, non septata, capitulo instrata. Stroma stilbiforme, sporidia eadem quae Fusidiorum. Contextus stromatis, uti videtur, tenue floccosus, floccis parallelis. Capitulum sub microscopio composito, aqua*

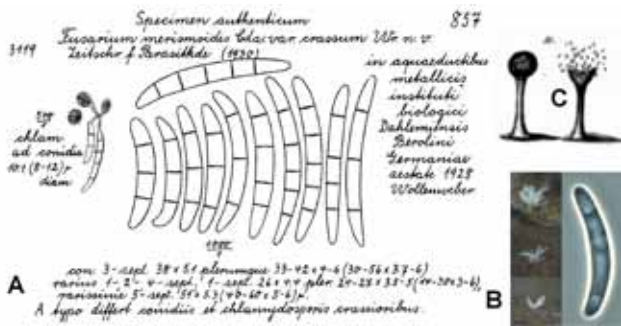


Fig. 2. *Atractium* species. A. *Atractium crassum*, as illustrated in the protologue by Wollenweber (1930). B. *Atractium stilbaster*, original drawing by Ditmar accompanying the protologue of *Atractium*, designated here as lectotype for *A. stilbaster*. C. *Atractium crassum*, digital photographs of living conidiomata (left) and a conidium (right) from a collection made in Ontario, Canada (K.A.S. 809).

adfusa, in sporidia fere diffluit. Unica species, nondum descripta. *A. stilbaster*, stipite cylindrico, capitulo globoso, utroque glabro lutescente. In truncis fagorum caesorum occurrit, vix ultra ½ lin. longa, fugax, stipite facili evanescente et capitulo in sporidia diffluente. 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 capitate, 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 reinterpretations 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 capitate, 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. eichleriana*. This species produces slimy, obovate to obclavate conidia that are usually curved, from long phialides on branched conidiophores. The present concept includes specimens with predominantly aseptate 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. stilbaster*, applying *Atractium* 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 *Chaetospora*, *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 teleomorphs 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 teleomorph 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 teleomorph of a species of *Fusicolla*, the macroconidia of which also occur on the specimen, rather than the teleomorph of *A. stilbaster*.

KEY TO ACCEPTED ATRACTIUM SPECIES

- 1. Conidia mostly (0-)1-3 septate; synnematous conidiomata produced 2
- 1. 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 |
|--|---|---------------|
| <i>A. aurantiacum</i> (Corda) Bonord. 1851 | Unknown | – |
| <i>A. brunaudiana</i> Sacc. 1883 | Unknown | – |
| <i>A. candiduli</i> Sacc. 1883 | = <i>Cylindrocarpon candidulum</i> (Sacc.) Wollenw. | – |
| <i>A. ciliatum</i> Link 1816 | Basionym of " <i>Fusarium</i> " <i>ciliatum</i> (Link) Link | This paper |
| <i>A. cristatum</i> Demelius 1923 | Unknown | – |
| <i>A. cronartioides</i> Speg. 1883 | Unknown | – |
| <i>A. flammeolum</i> Höhn. 1915 | <i>Nomen dubium</i> | Seifert 1985a |
| <i>A. flammeum</i> Berk. & Ravenel 1854 | = <i>Microcera coccophila</i> Desm. | This paper |
| <i>A. flavoviride</i> Sacc. 1883 | Synonym of <i>A. stilbaster</i> | Seifert 1985a |
| <i>A. fuscum</i> Sacc. 1883 | Synonym of <i>A. stilbaster</i> | Seifert 1985a |
| <i>A. gelatinosum</i> (Pers.) Sacc. 1886 | No type in L, <i>nomen dubium</i> | Seifert 1985a |
| <i>A. indicum</i> Chona & Munjal 1956 | Unknown | – |
| <i>A. lusitanicum</i> Sousa da Câmara & Luz 1941 | Unknown | – |
| <i>A. micropus</i> (Pers.) Sacc. 1886 | No type in L, <i>nomen dubium</i> | Seifert 1985a |
| <i>A. olivaceum</i> Kunze & J.C. Schmidt 1817 | No type in B, <i>nomen dubium</i> | Seifert 1985a |
| <i>A. pallens</i> Nees 1818 | Type in B examined, is a coelomycete | This paper |
| <i>A. pallidum</i> Bonord. 1851 | Unknown | – |
| <i>A. pallidum</i> Berk. & M.A. Curtis 1868 | Unknown | – |
| <i>A. pulvinatum</i> Link 1816 | Type in B examined, not an <i>Atractium</i> | This paper |
| <i>A. rigidum</i> Bonord. 1864 | Unknown | – |
| <i>A. stilbaster</i> Link 1809 | Accepted species | This paper |
| <i>A. therryanum</i> Sacc. 1879 | Anamorph of <i>Dermea morthieri</i> (Fuckel) Nannf. | Groves 1946 |
| <i>A. trematis</i> Hansf. 1944 | Unknown | – |
| <i>A. tubericola</i> Sacc. & Peglion. 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 6(2): 106. 1825 (1824).

= *Atractium fuscum* Sacc., Syll. Fung. 2: 514. 1883.

≡ *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 (*act1*).

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 *Coremium*-like structures. The macroconidia are gently curved with a rounded to 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 his 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 conidiogenous 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.

Typification: Philippines, Negros Occidental, Bario Caliban, Caliban River, on submerged wood, Dec. 1994, K.D. Hyde & E. Arimas, **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** ellipsoidal, 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 *Nectriadiella* (a synonym of the anamorphically typified genus *Cylindrocladiella*) and *Chaetopsinectria* (a synonym of the anamorphically typified genus *Chaetopsina*). 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 redispersed 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.

Typification: Germany, near Laubach, on rotting pores of a polypore, Solms, *Fungi europaei* no. 459, **lectotype** BPI designated by Rossman *et al.* 1999.

Other material examined: Germany, Bayerischer Wald, Arberseewand, on hymenium of *Inonotus nodulosus* on *Fagus sylvatica*, Aug. 1967, W. Gams 680, CBS 341.70 = VKM F-2863; Kr. Plön, near Dobersdorf, on hymenium of *Inonotus radiatus* on *Alnus*, Oct. 1965, W. Gams 1104, CBS 343.70; Eifel, Geeser Wald near Gerolstein, on *Inonotus radiatus*, Sep. 1970, W. Gams, CBS 841.70; Eifel, Geeser Wald near Gerolstein, on *Inonotus radiatus*, Sep. 1970, W. Gams, CBS 983.70 = VKM F-2862; Neubrandenburg, Kleppelshager Forst near Friedland, on *Inonotus radiatus*, Oct. 1978, P. Hübsch H78/40, CBS 704.79; Bayern, on *Inonotus nodulosus*, dead crust, on fallen branch of *Fagus sylvatica*, 1993, T.R. Lohmeyer & R. Boesmiller 93/62, A.R. 2741 = BPI 802729 = CBS 114050; Nordrhein-Westfalen, Detmold, Krebssteich, 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.

Typification: Germany, Niedersachsen, near Wilhelmshaven, Neuenburger Urwald, on *Hypoxylon* sp., May 1965, W. Gams, **holotype** CBS H-6635, **ex-type** culture CBS 748.69 GenBank barcodes: HQ897725 (*rbp2*), HQ897862 (*acl1*).

Other material examined: Germany, Nordrhein-Westfalen, Kamen, Heerener Holz, on *Hypoxylon* on *Fagus*, Apr. 2007, T. Gräfenhan 2007-22, DAOM 235822; Nordrhein-Westfalen, Detmold, Externsteine, 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, *Netherlands J. Pl. Pathol.* 88: 76. 1982.

Typification: 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 heterotypic *Hypomyces berkeleyanus* Plowr. & Cooke (\equiv *Sphaerostilbella berkeleyana* (Plowr. & Cooke) Samuels & Candoussau), 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 for *Cosmospora berkeleyana* need to be re-evaluated (Fig. 1). These synonyms include *Acremonium butyri*, *Cephalosporium khandalense*, *Gliomastix lavitskiae*, *Nectria vilior*, and *N. 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 valsaceous 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.

\equiv *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 (*rp2*), HQ897866 (*acl1*).

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 as 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, Enkendorfer 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 (*rp2*), HQ897914 (*acl1*).

Other material examined: **Germany**, Kr.Plön, Dobersdorfer Wald, on *Inonotus radiatus* on *Alnus glutinosa*, 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 (*rp2*), HQ897860 (*acl1*).

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**, Poltava 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 18666 = CBS 530.68 = IMI 133984 = VKM F-1324. GenBank barcodes: HQ897726 (*rp2*), HQ897863 (*acl1*).

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, valsaceous 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. *Asci* 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* monopodialidic, subulate to subclavate, hyaline. *Microconidia* ellipsoidal to clavate, aseptate, hyaline, abundant. *Macroconidia*, if present, 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, 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 stromata 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: 21. 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. 1898.

≡ *Fusarium episphaeria* (Tode) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 32: 662. 1945.

≡ *Cosmospora episphaeria* (Tode : Fr.) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 121. 1999.

Typification: Origin unknown, **lectotype** designated by Booth (1959) in L 0112704, Herb. Lugd. Bat. 910267659 ex Herb. Persoon, **isotype** TNS.

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 *Diatrype* on *Crataegus* 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.

Coloniae in agar CMA perithecia fertilia, aurantiaco-rubra vel rubra formantes; perithecia pyriformia, papilla brevi praedita. Dialonectriae episphaeriae similia, ascosporis dilute brunneis, bicellularibus, (8.7–)9.7–11(–12.5) × (3.7–)4–4.5(–4.8) µm. Conidiophora primum phialides simplices ex hyphis orientes, deinde irregulariter ramosa, nonnumquam verticillata. Monophialides subulatae vel subclavatae, 8–20 × 1.5–2.3 µm. Conidia copiosa in pionnote conidiophorum aggregatorum vel in conidiophoris singulis, tenuitunicata, hyalina: microconidia ellipsoidea vel clavata, unicellularia, (3–)3.5–5(–6.5) × 1–1.5(–1.7) µm, fere copiosa; macroconidia plerumque 3–5-septata, 1-septata: 10–25 × 1.5–2 µm, 3-septata: (20–)30–42(–48) × (1.8–)2–2.5(–2.7) µm, 4–5-septata: (30–)37–43.5(–50) × (1.8–)2–2.5(–2.7) µm, 6–7-septata: 40–48(–52) × (2–)2.3–2.7 µm, subcylindrica, modice curvata, utrinque paulo angustata, sursum saepe paulo uncinata et plus minusve acutata; ad basim vix an non pedicellata. Coloniae in agar PDA lente crescentes, 25–30 mm diam. post 14 dies, dilute aurantiae vel griseo-aurantiae. Mycelium aerium absens vel appressum, pionnotes aurantia iuxta coloniam mediam. Corpora sclerotialia absentia.

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-growing 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* monopodialidic, 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* ellipsoidal to 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,

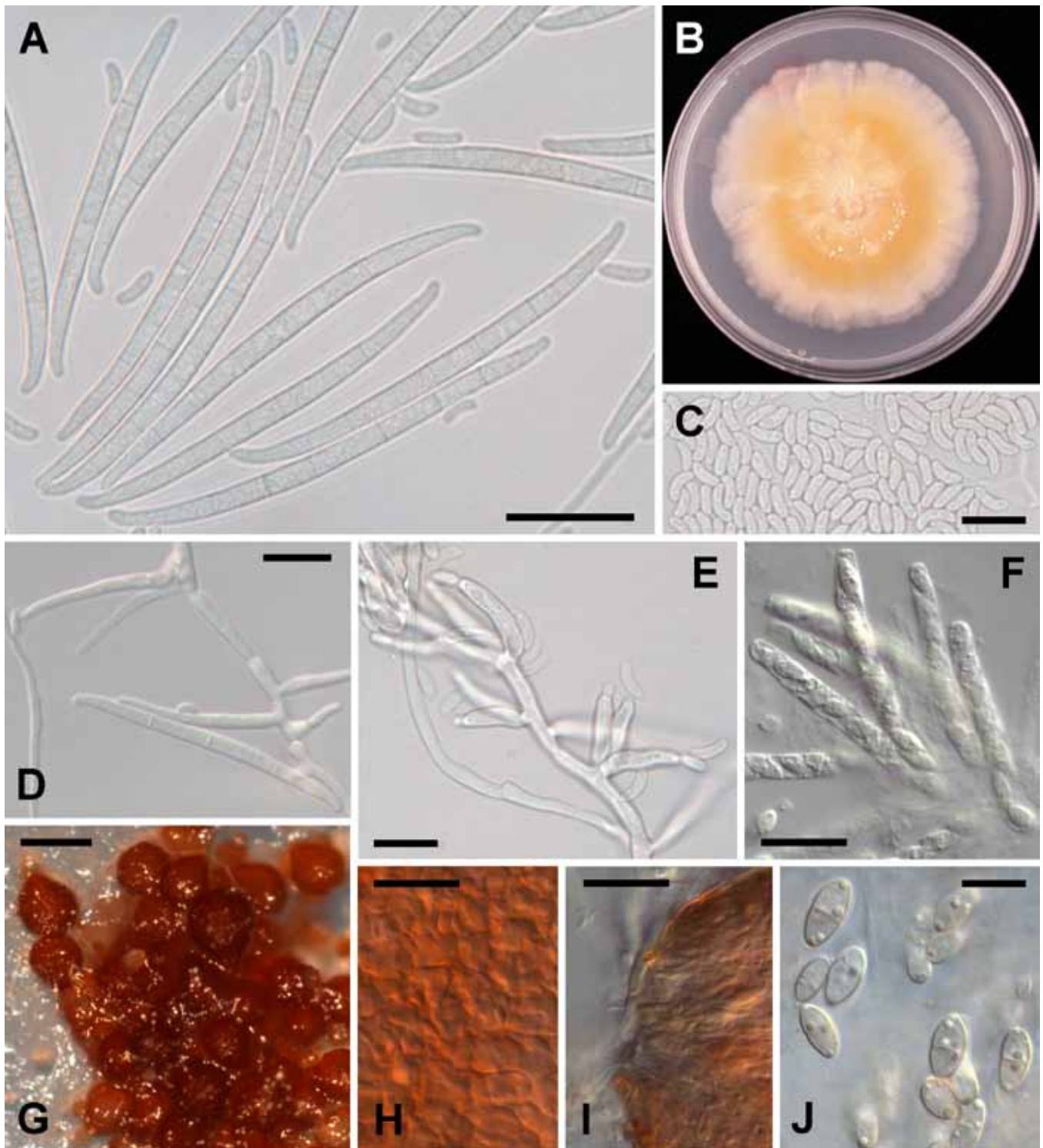


Fig. 3. A–J. *Dialonectria ullevolea*, ex-type strain (BBA 64549). A. Micro- and macroconidia formed on CMA after 18 d. B. Colony surface on PDA after 1 mo. C. Microconidia formed on CMA after 18 d. D–E. Phialides bearing microconidia on agar surface (D) and submerged (E) on CMA after 14 d. F. Cylindrical asci with obliquely uniseriate ascospores. G. Pyriform perithecia in culture on CMA after 50 d. H. Cells at surface of perithecial wall mounted in water. I. Perithecial apex mounted in water. J. Ascospores in optical section mounted in water. Scale bars: C, D, E, J = 10 μ m; A, F, H, I = 20 μ m; G = 200 μ m.

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 \times 1.5–2 μ m (n = 5), 3-septate: (20–)30–42(–48) \times (1.8–)2–2.5(–2.7) μ m (n = 40), 4–5-septate: (30–)37–43.5(–50) \times (1.8–)2–2.5(–2.7) μ m (n = 30), 6–7-septate: 40–48(–52) \times (2–)2.3–2.7 μ m (n = 25). *Chlamydoconidia* 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 (*act1*).

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.

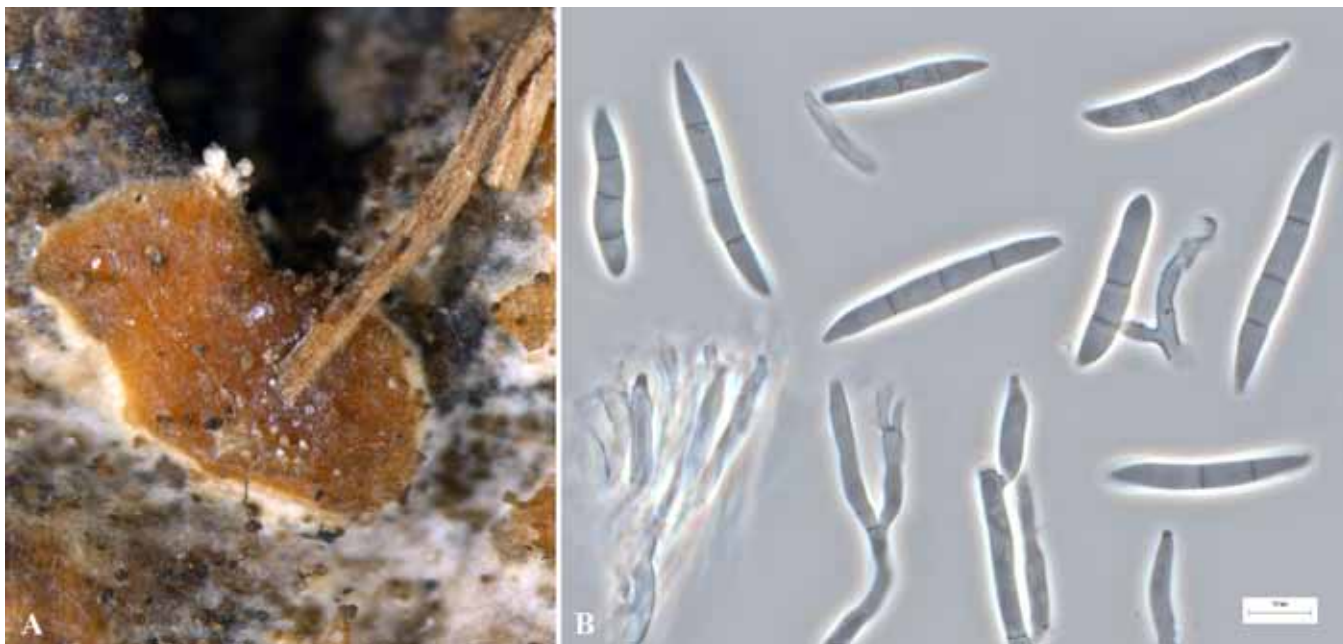


Fig. 4. *Fusicolla betae*, lectotype (K). A. Sporodochium. B. Conidia and phialides. Scale bar in B = 10 µm.

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 immersed. *Perithecia* scattered to gregarious, or in small groups, globose to pyriform with a short acute or disk-like papilla, pinched when dry, yellow, pale buff to orange, KOH–, smooth walled, usually 100–200 µm high. *Asci* cylindrical to narrowly clavate, with an apical ring, 8 uniseriate ascospores. *Ascospores* hyaline to pale brown, 1-septate, smooth or becoming slightly verrucose when mature. *Conidiophores* initially as lateral phialides on somatic hyphae, sometimes monochasial, verticillate or penicillate, hyaline. *Phialides* monopialidic, cylindrical to subulate, hyaline. *Microconidia* sparse or absent, ellipsoidal to allantoid, aseptate, hyaline. *Macroconidia* falcate, more or less straight, or moderately to clearly curved, slightly narrowing toward each end, apical cell often hooked with a more or less pointed tip, basal cell slightly pedicellate, predominantly 1–3-septate, or 3–5-septate, in one species up to 10-septate, hyaline, mostly thin-walled. *Chlamydoconidia* absent, sparse, or abundant, when present globose, single, in pairs or chains, sometimes in macroconidia.

Colonies 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: *Fusicolla* has generally been considered a synonym of *Fusarium* (see notes under *F. betae* below), but is adopted here for elements of the *F. aquaeductuum* and *F. merismoides* species complexes. Some of the varieties attributed to those two species by other authors are raised to species rank. The application of

the name *Fusarium merismoides* var. *chlamydosporale* remains uncertain at this time, while *F. merismoides* var. *crassum* is transferred to *Atractium* above.

Eight other species were described in *Fusicolla* before the genus was synonymised with *Fusarium* by 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.

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.

Typification: France, on tuber of *Beta vulgaris*, spring 1826, Desmazières, lectotype designated here K(M) 167520, *Plantae Cryptogames du Nord de la France*, no. 305; epitype designated here: Germany, Schleswig-Holstein, Kiel, on young plants of *Triticum aestivum*, Jan. 1983, C. Bauers, preserved culture BBA 64317. GenBank barcodes: HQ897781 (*rpb2*), HQ897917 (*act1*).

Other material identified: Germany, northern Germany, rotting potato tuber, E. Langerfeld DE 8, FRC E-0114 = MRC 2196 = NRRL 47186. Turkey, roots of *Papaver*, 2007, G. Turhan, T.G. 2007-70. UK, on *Beta vulgaris*, IMI 105043 = NRRL 22133.

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, no. 99, 100) probably studied type material of *Fusisporium betae*, but later listed the species as synonym of *Fusarium merismoides* irrespective of precedence of the older species epithet (Wollenweber & Reinking 1935). Following this, the genus *Fusicolla*

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 including *Fusisporium betae* as a synonym of *Cercospora apii* s. lat.; they also did not see type material (U. Braun, pers. comm.). Our studies 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 acetilerea (Tubaki, C. Booth & T. Harada) Gräfenhan & Seifert, **comb. et stat. nov.** MycoBank MB519434.

Basionym: *Fusarium merismoides* var. *acetilereum* 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 181488 = BBA 63789 = NRRL 20827. GenBank barcodes: HQ897701 (*rp2*), HQ897839 (*ac1*).

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, FRC E-0164 = 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 aquaeductuum (Radlk. & Rabenh.) Gräfenhan, Seifert & Schroers, **comb. nov.** MycoBank MB519435.

Basionym: *Selenosporium aquaeductuum* Radlk. & Rabenh., Kunst- Gewerbe-Blatt 49: 10. 1863.

≡ *Fusarium aquaeductuum* (Radlk. & Rabenh.) Lagerh., Centralbl. Bakteriol. Parasitenk. 9: 655. 1891.

Typification: **Germany**, Bayern, München, water fountain near Gasteigberg, 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 aquaeductuum*; it is the only known authentic material. **Epitype** designated here: **Germany**, Berlin-Dahlem, Julius-Kühn-Institute (formerly BBA), isol. ex plugged water tap in BBA, May 1985, H.I. Nirenberg, **ex-type** cultures BBA 64559 = CBS 837.85 = NRRL 20865 = NRRL 37595. GenBank barcodes: HQ897744 (*rp2*), HQ897880 (*ac1*).

Other material examined: **Germany**, Berlin, drinking water, 1974, W. Gerlach, BBA 63669 = CBS 734.79 = NRRL 20686; **The Netherlands**, Baarn, rubber tubing, 1953, 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 aquaeductuum*, 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. aquaeductuum with 1-septate conidia, 18–22 × 1.5–2 µm and *F. biasoletianum* with 3-septate conidia, 30–55 × 2–2.5 µm. Based on similarities of the phenotype and substrate preferences, we classify *Fusarium aquaeductuum* in *Fusicolla*.

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

Wollenweber (1931) linked *Fusarium aquaeductuum* var. *aquaeductuum* to "*Nectria*" *episphaeria* 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 (Höhn.) 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* (Höhn.) 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, Aberford & Gundle, on *Diatrypella* on *Betula*, Apr. 1961, C. Booth, IMI 85601, **ex-type** cultures ATCC 24369 = BBA 62201 = NRRL 20461 = NRRL 20439. GenBank barcodes: HQ897765 (*rp2*), HQ897901 (*ac1*).

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

Notes: For descriptions, illustrations, and discussion of the micro- and 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– ascumatal 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 (1959) and Samuels *et al.* (1991) concluded that *D. epistroma* is the anamorph of *N. magnusiana*, both being host specific to *Diatrypella favacea*. Only a few *Fusarium*-like macroconidia were found on the type material of *Dendrodochium epistroma*, but macroconidia were lacking on the hymenium 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 matuoi* (Hosoya & Tubaki) Gräfenhan & Seifert, comb. nov.** MycoBank MB519437.

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

= *Cosmospora matuoi* 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., Mamurogawa-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. **Japan**, on *Albizia julibrissin*, Oct. 1959, T. Kobayashi, ATCC 18694 = CBS 581.78 = MAFF 238445 = NRRL 20427.

Notes: For a description, illustrations, and discussion of the teleomorph 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 *et al.* 1983, Leslie *et al.* 2006, Domsch *et al.* 2007); these authors provide descriptions, illustrations, and discussion of the macroconidial anamorph of this species. The morphological species concept was established by Wollenweber & Reinking (1935), who synonymised numerous taxa with *Fusarium merismoides* var. *merismoides*. Unlike *F. betae*, 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

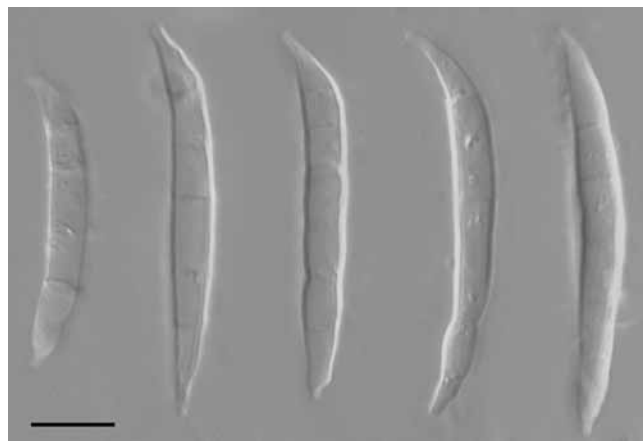


Fig. 5. *Fusarium biasolettianum*, authentic material (PRM 155487). Macroconidia. Scale bar = 10 µm.

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 *Chrysogluen 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. Biasoletto.

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 *Quadrastipidiotus perniciosus* (San José insect) scaleon dying 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 this species, 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 typica".

***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. *Microconidia* absent or very rare, when present ellipsoidal to allantoid, hyaline. *Macroconidia* 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 pionnotes.

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 *Macroconia* to generic rank here for five species with large *Fusarium*-like macroconidia and minute perithecia.

Accepted species

***Macroconia leptosphaeriae* (Niessl) Gräfenhan & Schroers, comb. nov.** MycoBank MB519442.

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

≡ *Cucurbitaria leptosphaeriae* (Niessl) O. Kuntze, Rev. Gen. Plant. 3: 461. 1898.

≡ *Hypomyces leptosphaeriae* (Niessl) Wollenw., Fus. autogr. del., Edn 1: No. 57. 1916.

≡ *Lasionectria leptosphaeriae* (Niessl) Petch, Trans. Brit. Mycol. Soc. 21: 267. 1938.

≡ *Cosmospora leptosphaeriae* (Niessl) Rossman & Samuels in Rossman, 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 *Leptosphaeria doliolum* on stems of *Urtica dioica*, Sept. & Oct. 1885, W. Krieger, Krieger's Fungi saxonici 165, **lectotype** designated here K(M) 165805, **isotype** B, BPI, K.

Other material examined: **Canada**, Ontario, Ottawa, Britannia, near Mud Lake, on *Leptosphaeria* on dead stem of *Urtica dioica*, July 2008, T. Gräfenhan 2008-15, DAOM 235833. **Italy**, Latio, ancient Etruscan village Corviano near Bomarzo, on *Leptosphaeria* on dead stem of *Urtica dioica*, Aug. 2008, T. Gräfenhan 2008-19, DAOM 235834. **The Netherlands**, Tilburg, on *Leptosphaeria* on dead stem of *Urtica dioica*, L. Rommelaars, CBS 100001, CBS-H 6030.

Notes: For description and illustration of the macroconidial anamorph and teleomorph of this species, see Weese (1916), Wollenweber (1916, No. 57; 1926; 1930, No. 859), Booth (1959, 1971), and Samuels *et al.* (1991).

The distinction between *Macroconia leptosphaeriae* and *M. sphaeriae* is based on the size of ascospores and conidia in the type collections. According to Wollenweber (1926), the ascospores of the type material of *M. leptosphaeriae* are smaller (14–18 × 5–5.5 µm) than those of *M. sphaeriae* (19–25 × 5.8–6.5 µm). These observations were partly confirmed by Samuels *et al.* (1991), who discussed the history and synonymy of the species. Five-septate conidia of *M. leptosphaeriae* measure 74–105 × 5–7 µm, whereas 5-septate conidia of *M. sphaeriae* are 45–73 × 4.5–5.5 µm (Wollenweber 1926). Further morphological studies of fresh collections from *Leptosphaeria* on *Urtica* are needed to confirm these species boundaries in these two species of *Macroconia*. Also, the occurrence of cellular hairs or sterile appendages on ascomatal

walls needs to be reviewed critically. Therefore, we refrain from designating epitype material for *M. leptosphaeriae* here.

***Macroconia cupularis* (J. Luo & W.Y. Zhuang) Gräfenhan & Seifert, comb. nov.** MycoBank MB519443.

Basionym: *Cosmospora cupularis* J. Luo & W.Y. Zhuang, Fungal Diversity 31: 88. 2008.

Typification: **China**, Zhejiang, Hangzhou, Taihuyuan, 500 m alt., on fruitbodies of a black ascomycete (*Stylothis* sp.) on twigs of an unidentified tree, Sep. 2005, J. Luo and W.Y. Li 6790-2, **holotype** HMAS 97514, **ex-type** culture HMAS 173240. GenBank barcodes: EF121864 (*ITS*), EF121870 (*28S rDNA*).

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

***Macroconia 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. 1886.

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 99592, **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 *Macroconia* is inferred from the morphology and sequences provided in the protologue, although we did not include the species in our own analysis.

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

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

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

? = *Fusarium gigas* Speg., Anales Soc. Ci. Argent. 22: 221. 1886.

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

Other material examined: **USA**, Florida, Tampa, near Hillsborough River State Park, on pyrenomycete on *Fabaceae*, Dec. 2006, T. Gräfenhan 2007-03, CBS 125495 = DAOM 238119.

Notes: For a description, illustrations, and discussion of the teleomorph, 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 *Bambusaceae*, Jan. 1882, B. Balansa, Pl. du Paraguay 3471, Spegazzini'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. Nassauischen Vereins Naturk. 23–24: 370. 1870.

? = *Nectria leptosphaeriae* var. *macrospora* Wollenw., Angew. Bot. 8: 187. 1926.

Typification: **Germany**, Hessen, Rheingau, Reichartshausen 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. Barbey-Boissier 2634.

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 epithet into a teleomorphically typified genus, resulting in a valid, legitimate but technically incorrect name under the present Art. 59.

Macroconia sphaeriae can be distinguished from *M. leptosphaeriae* 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.

Stroma 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 conidiogenous 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* monopialidic, flask shaped, hyaline, usually with obvious periclinal thickening and inconspicuous collarettes. *Conidia* aseptate, hyaline, in imbricate chains that eventually collapse to form slimy heads. *Chlamydozoospores* 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 conidiogenous 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 Rossman *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* (HQ843766) differs by 5 substitutions from *N. mariannaea*, and 3 substitutions from *M. aquaticicola*. Thus, given the limited amount of variation in the ITS and LSU normally seen in the *Nectriaceae*, the phylogenetic data suggest that *M. aquaticicola*, *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. aquaticicola*, *M. camptospora*, 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.

Coloniae in agar malti et peptono confecto post 7 dies 21 mm diam, aureo-brunneae vel brunneo-aurantiae; in agar farina avenae confecto 28–29 mm diam, sub luce aurantio-griseae, obscuritate griseo-aurantiae. Conidiophora 100–200 µm longa, stipite 2–3.5 µm lato, bis vel ter verticillata, verticillos terminales (2–)3–5 phialidum, in verticillis subterminalibus 25–35 µm distantibus 1–3 phialides ferentia; raro phialides singulae circa 20 µm longae ex hyphis repentibus orientes. Phialides 12–30 µm longae, in parte latissima 2–3.5 µm latae, subulate, in summo periclinally inspissatae, collari inconspicuo cylindrico praeditae. Conidia 3.5–7.5 × 2.5–3.5 µm, late fusiformia vel ellipsoidea, symmetrica, sed saepe asymmetrica ex apertura conidiogena protrusa, hyalina, levia, in catenis imbricatis saepe collabentibus adhaerentia. Holotypus DAOM 235814 (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 ellipsoidal, 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. *Chlamydozoospores* rarely produced, globose to ellipsoidal, 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 (5–6D6) 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)

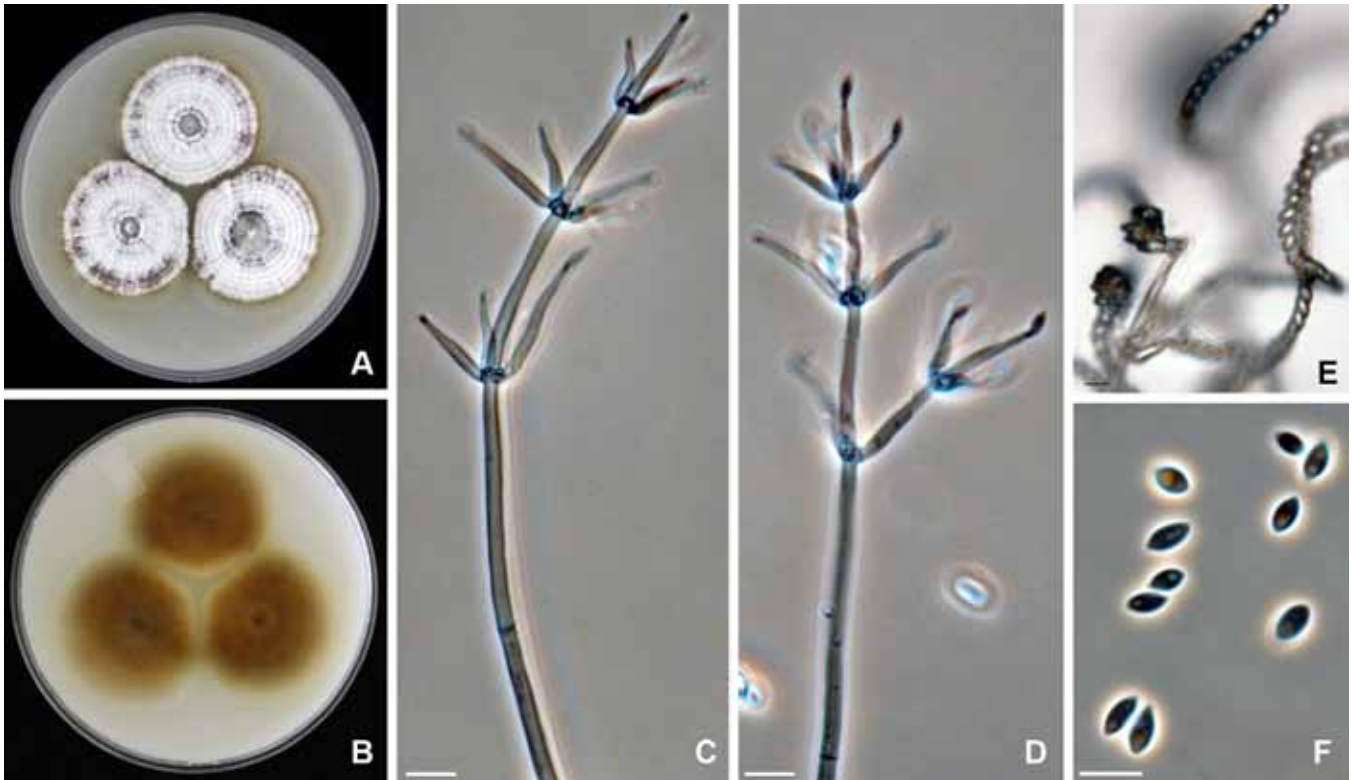


Fig. 6. *Mariannaea samuelsii*, ex-type strain. A, B. Obverse and reverse of 14 d old colony on oatmeal agar. C, D. Conidiophores showing verticillate branching. E. Imbricate conidial chains. F. Conidia. Scale bars = 10 μ m.

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 (*act1*).

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 \times 2.5–3.5 μ m) intermediate in length between the shorter conidia of *M. elegans* (4–6 \times 1.5–2.5 μ m) and the longer conidia of *M. aquaticola* (5–10 \times 2–4.5 μ m). *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 μ m 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 monochasial, verticillate to penicillate, hyaline, usually forming discrete sporodochia or synnemata on the host. **Phialides** monopodialic, cylindrical to subulate to subclavate, hyaline. **Microconidia** absent. **Macroconidia** 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 synnematus *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

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 |
|---|--|-----------------------------|
| <i>M. acuminata</i> (Ellis & Everh.) Höhn. 1919 | = <i>Fusarium acuminatum</i> | Wollenweber & Reinking 1935 |
| <i>M. auranticola</i> Petch 1921 | = <i>M. larvarum</i> | This paper |
| <i>M. brachyspora</i> Sacc. & Scalia 1904 | ? = <i>Fusicolla aquaeductuum</i> | Wollenweber & Reinking 1935 |
| <i>M. ciliata</i> (Link) Wollenw. 1916 | = " <i>Fusarium</i> " <i>ciliatum</i> , status unclear | – |
| <i>M. clavariella</i> Speg. 1886 | = <i>Cladosterigma fuispora</i> Pat. | Seifert 1985b |
| <i>M. coccidophthora</i> Petch 1921 | = <i>Fusarium tasmanicum</i> (McAlpine) Rossman 1983 | Rossman 1983 |
| <i>M. coccophila</i> Desm. 1848 | Accepted species | This paper |
| <i>M. curta</i> Sacc. 1909 | = <i>M. larvarum</i> | This paper |
| <i>M. erumpens</i> Ellis & Everh. 1894 | Unknown | – |
| <i>M. fujikuroi</i> Miyabe & Sawada 1913 | = <i>M. diploa</i> | This paper |
| <i>M. henningsii</i> (Koord.) Petch 1914 | = <i>M. diploa</i> | This paper |
| <i>M. massariae</i> Sacc. 1886 | = " <i>Fusarium</i> " <i>ciliatum</i> , see above | Wollenweber & Reinking 1935 |
| <i>M. merrillii</i> Syd. 1914 | = <i>M. diploa</i> | This paper |
| <i>M. mytilaspidis</i> McAlpine 1904 | = <i>Fusarium lateritium</i> var. <i>longum</i> | Wollenweber & Reinking 1935 |
| <i>M. orthospora</i> Syd. 1924 | = <i>Mycogloea orthospora</i> (Syd.) R. McNabb ex Dingley 1989 | Dingley 1989 |
| <i>M. parlatoriae</i> Trab. 1907 | = <i>M. larvarum</i> | This paper |
| <i>M. pluriseptata</i> Cooke & Massee 1888 | = <i>M. coccophila</i> | This paper |
| <i>M. rectispora</i> Cooke & Massee | = <i>Tetracrium rectisporum</i> (Cooke & Massee) Petch 1921 | Petch 1921 |
| <i>M. tasmanica</i> McAlpine 1904 | = <i>Fusarium tasmanicum</i> (McAlpine) Rossman 1983 | Rossman 1983 |
| <i>M. tonduzii</i> Pat. 1912 | = <i>M. larvarum</i> | This paper |

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 "*Stilbum*" 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*, *Fusisporium*, *Fusoma*, *Microcera*, *Pionnotes*, *Pseudomicrocera*, and *Selenosporium* 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, *Plantes Cryptogames de France*, Ed. II, Ser. I, No. 1350, **isotypes** P, K (M) 165806, *Plantes Cryptogames de France* Ed. I, Ser. I, No. 1750.

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

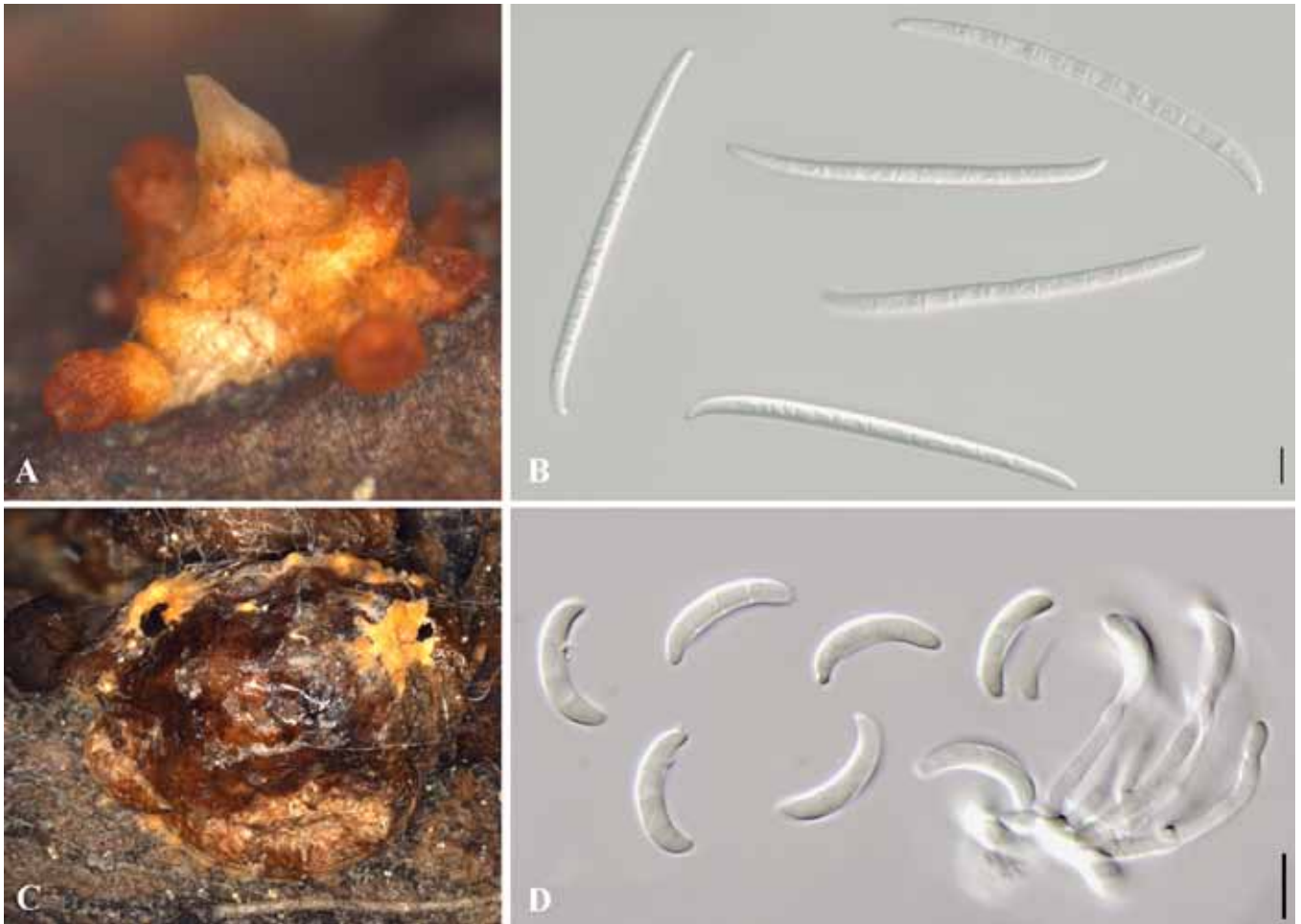


Fig. 7. Two *Microcera* species. A, B. *Microcera coccophila*. A. Habit, with conical red perithecia on a stroma growing over scale insect and flame-like synnema emerging from the top. B. Macroconidia. C, D. *M. larvarum*. C. Flame-like conidiomata on scale insect. D. Conidia. Scale bars = 10 µm.

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 aurantiicola*"). He cited two Desmazières exsiccata 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, 1981b, 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.

- ≡ *Cucurbitaria diploa* (Berk. & M.A. Curtis) O. Kuntze, *Rev. Gen. Plant.* 3: 461. 1898.
- ≡ *Creonectria diploa* (Berk. & M.A. Curtis) Seaver, *Mycologia* 1: 190. 1909.
- ≡ *Calonectriadiploa* (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* Henn. [as "*coccideicola*"], *Bot. Jahrb. Syst.* 34: 57. 1904.
- = *Aschersonia henningsii* Koord., *Bot. Untersuch. Java* p. 213. 1907.
- ≡ *Microcera henningsii* (Koord.) Petch, *Ann. Roy. Bot. Gard. Peradeniya* 5: 533. 1914.
- ≡ *Pseudomicrocera henningsii* (Koord.) Petch, *Trans. Brit. Mycol. Soc.* 7: 164. 1921.
- = *Microcera fujikuroi* Miyabe & Sawada, *J. Coll. Agric. Tohoku Imp. Univ.* 5: 83. 1913.
- = *Microcera merrillii* Syd., *Ann. Mycol.* 12: 576. 1914.

Typification: **Cuba**, on individual scale insects on bark, C. Wright 606 ex Herb. Berk., *Fungi Cubensis Wrightiana* 767, **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. juruanum*, and *F. pentaclethrae*, which were described only from herbaceous material (Wollenweber & Reinking 1935). We studied Hennings' material (*F. derridis* = B 700014017; *F. juruanum* = B 700014035, B 700014036; *F. pentaclethrae* = B 700014037), and none seem to be insect-associated. Therefore, we reject these synonymies, except for *F. coccidicola* as listed above.

Microcera larvarum (Fuckel) Gräfenhan, Seifert & Schroers, **comb. nov.** MycoBank MB519449. 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 tonduzii* Pat., Bull. Soc. Mycol. France 28: 142. 1912.
- = *Microcera aurantiicola* 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 00111015 **Epitype** designated here: **Iran**, Prov. Gilan, near Rasht, on *Quadraspidiotus perniciosus* (San José insect) scale on *Prunus domestica*, Oct. 1968, W. Gerlach & D. Ershad, **epitype** BBA, **ex-type** cultures BBA 62239 = CBS 738.79 = MUCL 19033 = NRRL 20473. GenBank barcodes: HQ897768 (*rp2*), HQ897904 (*acl1*).

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 parnafungin 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 aurantiicola*" cited by Booth (1971, 1981a), Gerlach & Nirenberg (1982), and Rossman *et al.* (1999) should be critically reviewed.

Microcera rubra Gräfenhan & Seifert, **sp. nov.** MycoBank MB519450.

- = *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 *Quadraspidiotus perniciosus* (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 (*rp2*), HQ897903 (*acl1*).

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 *Atractium*. 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* 1932. 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. rusci*", remains unresolved.

Pseudonectria buxi (DC.) Seifert, Gräfenhan & Schroers, **comb. nov.** MycoBank MB519451.

Basionym: *Tubercularia 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

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. *Asci* 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. *Conidiophores* 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 collarete. *Microconidia* 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 margin smooth to broadly lobed

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

Notes: *Stylonectria* was described by Höhnelt (1915) as an anamorph genus with the type and only species, *S. applanata*, for which the teleomorph was considered to be "*Nectria*" *applanata* var. *succinea*. Booth (1959) presented convincing evidence that Höhnelt (1915) actually was dealing with a teleomorphic fungus, which was further explained by Rossman *et al.* (1999). Species of *Stylonectria* are considered to be host specific, probably to the fungal host, which itself may be host specific to the plant.

Accepted species

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

= *Nectria applanata* var. *succinea* Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Wien, Math.-Naturwiss. Kl., Abt. 1, 124: 51. 1915.

Typification: **Austria**, Niederösterreich, near Sonntagsberg, on stromata of *Melogramma bulliardii* on dead twigs of *Corylus avellana*, Aug. 1914, P. Strasser, **lectotype** designated here FH 00286663.

Notes: For descriptions and discussion of the teleomorph, microconidial anamorph, and macroconidial synanamorph of this species, see von Höhnelt (1915) and Weese (1916).

Von Höhnelt (1915) distinguished "*Nectria*" *applanata* var. *succinea* from "*N.*" *applanata* var. *applanata* based on the pale yellow colour of the translucent perithecia. Otherwise, the two varieties were described with identical macro- and microscopic characters. Because host specificity is an important character for distinguishing species of *Stylonectria* (*cf.* Gräfenhan 2009), we recognise *S. applanata* as a distinct species from *S. carpini*, described below, *i.e.* *Nectria applanata* var. *applanata*.

Stylonectria carpini Gräfenhan, **nom. nov.** MycoBank MB519452.

= *Nectria applanata* Fuckel, Jahrb. Nassauischen Vereins Naturk. 25–26: 310. 1871 (1872).

= *Cucurbitaria applanata* (Fuckel) O. Kuntze, Rev. Gen. Plant. 3: 460. 1898.

= *Dialonectria applanata* (Fuckel) Petch, Trans. Brit. Mycol. Soc. 25: 170. 1941.

Etymology: The species epithet is derived from the plant host genus *Carpinus*.

Typification: **Germany**, Hessen, Rheingau, Aepfelbach im Oestricherwald, on black pyrenomycete on decaying, corticated branches of *Carpinus betulus*, L. Fuckel, Fuckel Fungi Rhenani 2356, **lectotype** designated here G 00111018, **isotypes** B 700014054, FH 00286648, K, DAOM 119800 = Herb. Barbey-Boissier 862.

Other material examined: **Austria**, Niederösterreich, Gießhübl, Wasserspreng, Talgrund, (Finsterer Gang), MTB 7863/1, on *Melanconis spodiaea* on *Carpinus betulus*, Aug. 2006, H. Voglmayr W.J. 3013, DAOM 235819. **Germany**, Schleswig-Holstein, near Stegelkamp, Naturwaldzelle Endern, on pyrenomycete on *Carpinus betulus*, Aug. 2008, T. Gräfenhan 2008-17, DAOM 235829.

Notes: This species produces both a micro- and a macroconidial synanamorph in addition to a teleomorph. Our examination of Höhnelt's type material of *Stylonectria applanata* (FH 00286663) and that of Fuckel's "*Nectria*" *applanata* (G 00111018) 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 betulinus* 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: *Sphaeria purtonii* Grev., Scot. Crypt. Fl. 6: 23. 1828.

= *Nectria purtonii* (Grev.) Berk., Outl. Brit. Fung. p. 394. 1860.

= *Dialonectria purtonii* (Grev.) Cooke, Grevillea 12: 110. 1884.

= *Cucurbitaria purtonii* (Grev.) O. Kuntze, Rev. Gen. Plant. 3: 461. 1898.

= *Cosmospora purtonii* (Grev.) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 124. 1999.

Typification: **UK**, Scotland, Edinburgh, Rossllyn Woods, on black pyrenomycete on small branches of coniferous tree, 1820, Greville, **lectotype** E designated by Booth 1958.

Other material examined: **France**, Provence, St. Remy, on old stromata of pyrenomycete on *Coronilla emerus*, Oct. 1974, W. Gams, culture CBS 717.74. **Germany**, Nordrhein-Westfalen, Detmold, Externsteine, on small branches of felled trees of *Picea abies*, Apr. 2007, T. Gräfenhan 2007-30, DAOM 235818.

Notes: For descriptions, illustrations, and further taxonomic synonyms of the teleomorph as well as microconidial and macroconidial synanamorphs of this species, see Booth (1959) and Samuels (1976).

Stylonectria wegeliniana (Rehm) Gräfenhan, Voglmayr & Jaklitsch, **comb. nov.** MycoBank MB519454.

Basionym: *Nectria episphaeria* var. *wegeliniana* Rehm, Hewigia 30: 260. 1891.

= *Dialonectria wegeliniana* (Rehm) Petch, Trans. Brit. Mycol. Soc. 21: 266. 1938 as *D. wegeliana*.

= *Cosmospora wegeliniana* (Rehm) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 131. 1999.

Typification: Switzerland, Heimiswyl bridge near Bern, on *Hapalocystis bicaudata* (= *Pseudovalsa berkeleyi*) on dry branches of *Ulmus*, Oct. 1887, Wegelin, Rehm Ascomyceten 1045, **lectotype** designated here S F86597, **isotype** NY.

Other material examined: Austria, Niederösterreich, Distr. Mödling, Comm. Hinterbrühl, Wassergspreng, Finsterer Gang west of Gießhübl, 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 µm 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 uniseriate or partially biseriate near base, completely filling each ascus. *Conidiophores* aggregated into sporodochia or synnemata, with an inconspicuous basal stroma; unbranched, hyaline setae around margin of conidiomata. *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* monophialidic, 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 synanamorph 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 conidiomata. 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 conidiomata 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 clade 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 teleomorphs associated with *Volutella* provide clues to its polyphyly. "*Cosmospora*" *consors* was reported as the teleomorph 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 synnematosus fungus *V. citrinella* was formerly known as *Stilbella aciculosa* (Seifert 1985a) but is more appropriately classified in *Volutella*. There have been scattered comments in the literature about synnematosus species of *Volutella*, including the comment by Domsch *et al.* (2007) that some strains or species are "short stipitate". Thus, the inclusion of synnematosus species only subtly alters the existing generic concept. Although there was scant mention of *Volutella* in the monograph of the synnematosus 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.

Typification: 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, Gräfenhan & Schroers, **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 comata* Ellis, Bull. Torrey Bot. Club 9: 20. 1892.

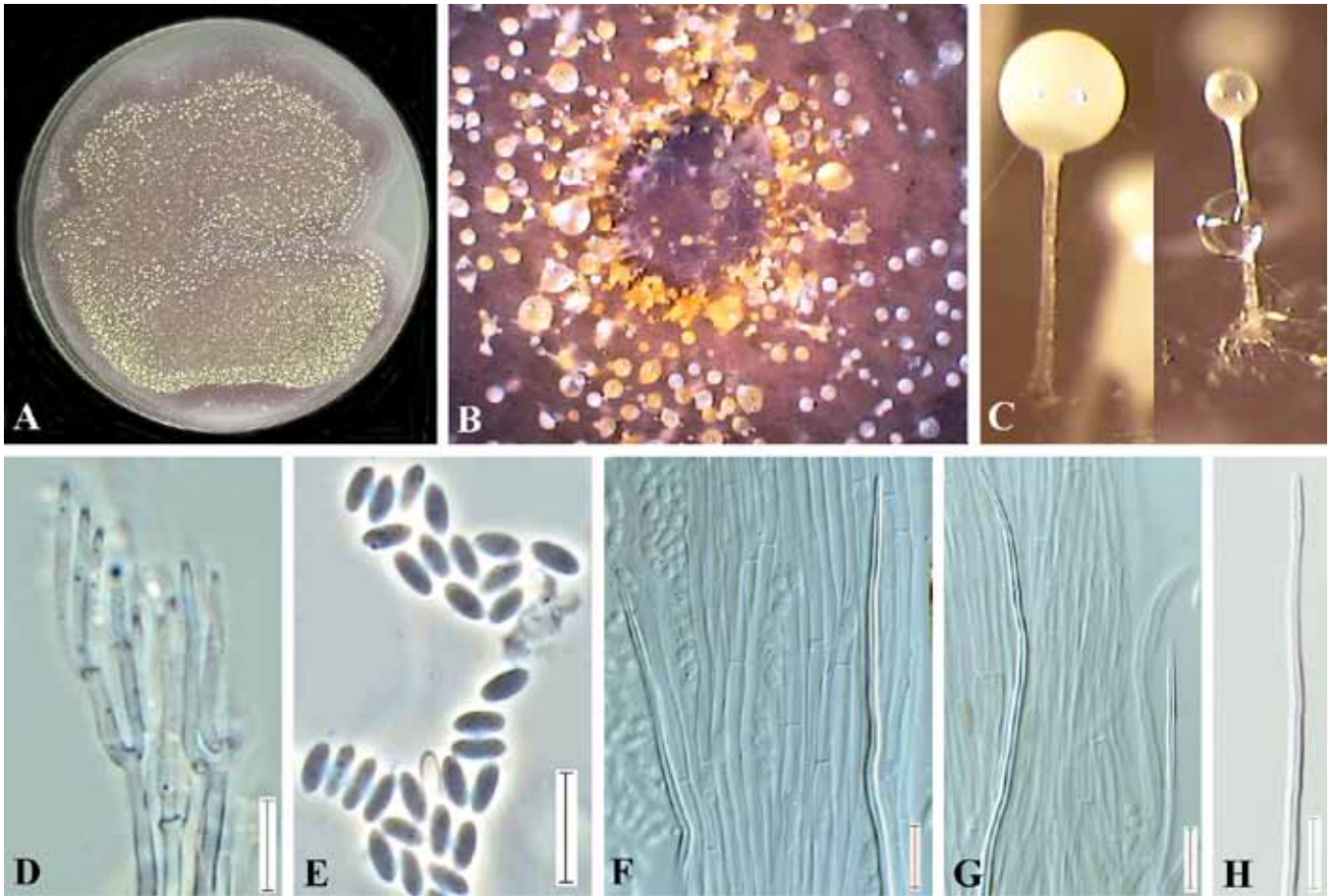


Fig. 8. *Volutella citrinella*, colony and microscopic characters. A, B. Colony on oatmeal agar showing typical purple pigment and yellowish slime of the synnemata. C, D. Determinate synnemata developed in culture. E. Conidiophores. F. Conidia. G, H, I. Seta-like marginal hypha in culture (DAOM 226716, 165570). Scale bars = 10 µm.

? = *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 synanamorphs 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 & Masee) Seifert, **comb. nov.** MycoBank MB519456. Fig. 8.

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

= *Stilbum 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.

= *Nectria stilbellae* Samuels & Seifert, *Sydowia* 43: 250. 1991.

≡ *Cosmospora stilbellae* (Samuels & Seifert) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, *Stud. Mycol.* 42: 125. 1999.

For other synonyms, see Seifert (1985a) under *Stilbella aciculosa*.

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 thickened 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.

ACKNOWLEDGEMENTS

This study would have been impossible without the tremendous contributions of Gary J. Samuels. His habit of sharing collections selflessly and his holistic approach to describing fungi make him a role model for both beginning and experienced mycologists. He could have been easily a co-author of this study, but then we could not have written this acknowledgement for him!

We thank Kerry O'Donnell for providing unpublished DNA sequences (*rpb2*) for many *Fusicolla* and *Microcera* strains deposited with NRRL. We enjoyed numerous fruitful discussions with Scott Redhead on interpretations of Article 59 of the ICBN but assume full responsibility for the nomenclatural decisions made here. We thank the curators of the herbaria B, DAOM, G, FH, K, L, PAD, PH, PRM, S, and UPS for the loan of type and other material or for searching for relevant material. We are especially indebted to Harrie Sipman at the Botanical Museum in Berlin for providing information on fungal specimens deposited by H. Richter and H.W. Wollenweber.

We appreciate the continued support of and consultation with our mentor Prof. W. Gams, who prepared the Latin diagnosis for *M. samuelsii*, while proclaiming his horror at the nomenclatural mutations proposed here by his devoted former students.

We are grateful for DNA sequencing by Gerry Louis-Seize, and for the support from the Canadian Collection of Fungal Cultures. Last but not least, we thank W. Jaklitsch and H. Voglmayr for permission to study their specimens of *Stylonectria* and the examination of type material of *S. wegeliniana*.

REFERENCES

- Akaike H (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**: 716–723.
- Beyma van FH (1938). Beschreibung einiger neuer Pilzarten aus dem "Centraalbureau voor Schimmelcultures" Baarn (Holland). *Zentralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten, 2. Abt.* **99**: 381–394. [in German]
- Bezerra JL (1963). Studies on *Pseudonectria roussei*. *Acta Botanica Neerlandica* **12**: 58–63.
- Bills GF, Platas G, Overy DP, Collado J, Fillola A, Jiménez MR, Martín J, del Val AG, Vicente F, Tormo JR, Peláez F, Calati K, Harris G, Parish C, Xu D, Roemer T (2009). Discovery of the pamafungins, antifungal metabolites that inhibit mRNA polyadenylation, from the *Fusarium larvarum* complex and other hypocrealean fungi. *Mycologia* **101**: 449–472.
- Booth C (1959). Studies of Pyrenomyces IV. *Nectria* (part I). *Mycological Papers* **73**: 1–115.
- Booth C (1971). The genus *Fusarium*. 1–234. International Mycological Institute, Kew.
- Booth C (1981a). *Nectria aurantiicola*. *CMI Descriptions of pathogenic fungi and bacteria* **714**: 1–2.
- Booth C (1981b). *Nectria flammea*. *CMI Descriptions of pathogenic fungi and bacteria* **715**: 1–2.
- Booth C (1981c). Perfect states (teleomorphs) of *Fusarium* species. 446–452. In: *Fusarium: Disease, Biology, and Taxonomy* (Nelson PE, Toussoun TA, Cook RJ, eds.). The Pennsylvania State University Press, University Park and London.
- Brandes EW (1919). Banana wilt. *Phytopathology* **9**: 339–389.
- Carmichael JW, Kendrick WB, Conners IL, Sigler L (1980). Genera of Hyphomycetes. i–x, 1–386. Edmonton, Canada; University of Alberta Press.
- Chaverri P, Salgado C, Hirooka Y, Rossman AY, Samuels GJ (2011). Delimitation of *Neonectria* and *Cylindrocarpon* (*Nectriaceae*, *Hypocreales*, *Ascomycota*) and related genera with *Cylindrocarpon*-like anamorphs. *Studies in Mycology* **68**: 57–78 (this issue).
- Chupp C (1954). A monograph of the fungus genus *Cercospora*. 1–667. Ithaca, NY: Chupp.
- Crous PW, Braun U (2003). *Mycospherella* and its anamorphs. 1. Names published in *Cercospora* and *Passalora*. *CBS Biodiversity Series* **1**: 1–571.
- Crous PW, Braun U, Schubert K, Groenewald JZ (2007). Delimiting *Cladosporium* from morphologically similar genera. *Studies in Mycology* **58**: 33–56.
- Crous PW, Seifert KA (1998). Megaconidia as an additional taxonomic character in *Cylindrocladium*, with a note on *Cylindrocladiopsis*. *Fungal Diversity* **1**: 53–64.
- Cock AWAM de, Lévesque A (2004). New species of *Pythium* and *Phytophthora*. *Studies in Mycology* **50**: 481–488.
- Dingley JM (1951). The *Hypocreales* of New Zealand. II. The genus *Nectria*. *Journal of the Royal Society of New Zealand* **79**: 177–202.
- Dingley JM (1989). Reappraisal of *Microcera othospora* and *Myxosporium hoheriae*. *Memoirs of the New York Botanical Garden* **49**: 206–209.
- Dodge BO (1944). A new *Pseudonectria* on *Pachysandra*. *Mycologia* **36**: 532–537.
- Dodge CW (1935). Medical Mycology. C. V. Mosby Co., St. Louis.
- Domsch KH, Gams W, Anderson T (2007). Compendium of soil fungi. 2nd ed. 1–672. IHW-Verlag, Eching, Germany.
- Fryar SC, Booth W, Davies J, Hodgkiss JI, Hyde KD (2004). Distribution of fungi on wood in the Tutong River, Brunei. *Fungal Diversity* **17**: 17–38.
- Gams W (1971). *Cephalosporium*-artige Schimmelpilze (Hyphomycetes). 1–262. G. Fischer, Stuttgart.
- Gams W, Nirenberg HI (1989). A contribution to the generic definition of *Fusarium*. *Mycotaxon* **35**: 407–416.
- Gams W, Zaayen van A (1982). Contribution to the taxonomy and pathogenicity of fungicolous *Verticillium* species. I. Taxonomy. *Netherlands Journal of Plant Pathology* **88**: 57–78.
- Gerlach W (1972). Fusarien aus Trinkwasserleitungen. *Annales Agricolurae Fenniae* **11**: 298–302.
- Gerlach W (1977). Drei neue Varietäten von *Fusarium merismoides*, *F. larvarum* und *F. chlamydosporum*. *Phytopathologische Zeitschrift* **90**: 31–42.
- Gerlach W, Nirenberg HI (1982). The genus *Fusarium* — A pictorial atlas. *Mitteilungen der Biologischen Bundesanstalt für Land- und Forstwirtschaft* **209**: 1–406.
- Gräfenhan T (2009). Contributions to the taxonomy of the ascomycete genus *Cosmospora* and its anamorphs. *Zeitschrift für Mykologie* **75**: 175–188. [in German]
- Gräfenhan T, Nirenberg HI, Seifert KA (2008). The hidden diversity of *Cosmospora* and its *Fusarium* anamorphs. *Journal of Plant Pathology* **90** (3, Suppl.): S3.18.
- Groves JW (1946). The North American species of *Dermea*. *Mycologia* **38**: 352–431.
- Hall TA (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**: 95–98.
- Hirooka Y, Rossman AY, Chaverri P (2011). Morphological and phylogenetic revision of the *Nectria cinnabarina* species complex. *Studies in Mycology* **68**: 35–56 (this issue).
- Höhnelt F von (1909). Fragmente zur Mykologie: VI. Mitteilung (Nr. 182 bis 288). *Sitzungsberichte der mathematisch-naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften, Wien* **118**: 275–452.
- Höhnelt F von (1912). Fragmente zur Mykologie (XIV. Mitteilung, Nr. 719 bis 792). *Sitzungsberichte der mathematisch-naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften, Wien* **121**: 339–784.
- Höhnelt F von (1915). Fragmente zur Mykologie (XVII. Mitteilung, Nr. 876 bis 943). *Sitzungsberichte der mathematisch-naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften, Wien* **124**: 49–159.
- Holmgren PK, Holmgren NH, Barnett LC (1990). Index herbariorum. Part I: The herbaria of the world. 8th edition. New York Botanical Garden, New York.
- Holubová-Jechová V, Gams W, Nirenberg HI (1994). Revisiónes Generum Obscurorum Hyphomycetum: a revision of the *Selenosporium* species described by A.C.J. Corda. *Sydowia* **46**: 247–256.
- Hosoya T, Tubaki K (2004). *Fusarium matuoi* sp. nov. and its teleomorph *Cosmospora matuoi* sp. nov. *Mycoscience* **45**: 261–270.
- Jaap O (1910). Verzeichnis der bei Triglitz in der Prignitz beobachteten Ascomyceten. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg* **52**: 109–150.
- Karsten PA (1891). Symbolae ad mycologicam fennicam. Pars XXX. *Meddelanden af Societas pro Fauna et Flora Fennica* **18**: 61–74.
- Kornerup A, Wanscher JH (1978). Methuen handbook of colour, 3rd edition. 1–252. Eyre Methuen, London.
- Leslie JF, Summerell BA, Bullock S (2006). The *Fusarium* laboratory manual. 1–388. Blackwell Publishing, Ames, Oxford, and Victoria.
- Li C, Kurniawati E, Hyde KD (2009). Morphological and molecular characterization of *Mariannaea aquatica* sp. nov. collected from freshwater habitats. *Mycological Progress* **9**: 337–343.
- Liang Z-Q (1991). Determination and identification of anamorph of *Cordyceps pruinosa*. *Acta Mycologica Sinica* **10**: 72–80.
- Lindau G (1910). Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz. Zweite Auflage. Erster Band: Die Pilze Deutschlands, Österreichs und der Schweiz. X. Abteilung: Fungi imperfecti: Hyphomycetes (zweite Hälfte), Dematiaceae (Phaeophragmiae bis Phaeostauroporaee), Stilbaceae, Tuberculariaceae, sowie Nachträge, Nährpflanzenverzeichnis und Register. Leipzig.
- Link JHF (1816). Observationes in ordines plantarum naturales. Dissertatio secunda. *Magazin. Gesellschaft Naturforschender Freunde zu Berlin* **7**: 25–45.
- Link JHF (1825). *Caroli a Linne Species plantarum: exhibentes plantas rite cognitatas, ad genera relatas, cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas* **6**(2): 106. Impensis G. C. Nauk, Berolini.
- Liu Z-Y, Liang Z-Q, Liu A-Y, Yao Y-J, Hyde KD, Yu Z-N (2002). Molecular evidence for teleomorph–anamorph connections in *Cordyceps* based on ITS-5.8S rDNA sequences. *Mycological Research* **106**: 1100–1108.
- Lombard L, Crous PW, Wingfield BD, Wingfield MJ (2010). Systematics of *Calonectria*: a genus of root, shoot and foliar pathogens. *Studies in Mycology* **66**: 1–71.
- Luo J, Zhuang W-Y (2008). Two new species of *Cosmospora* (*Nectriaceae*, *Hypocreales*) from China. *Fungal Diversity* **31**: 83–93.
- Luo J, Zhuang W-Y (2010). *Chaetopsinectria* (*Nectriaceae*, *Hypocreales*), a new genus with *Chaetopsina* anamorphs. *Mycologia* **102**: 976–984.
- Lutzoni F, Kauff F, Cox CJ, McLaughlin D, Celio G, et al. (2004). Assembling the fungal tree of life: progress classification and evolution of subcellular traits. *American Journal of Botany* **91**: 1446–1480.
- Matsushima T (1975). *Icones Microfungorum a Matsushima lectorum*. 1–209. Published by the author, Kobe, Japan.

- Matsushima T (1980). Saprophytic microfungi from Taiwan. Part 1. Hyphomycetes. *Matsushima Mycological Memoirs* 1: 1–82.
- McAlpine D (1899). Fungus diseases of citrus trees in Australia, and their treatment. 1–132. Australia, Melbourne; Agriculture Department of Victoria.
- McAlpine D (1904). Two new fungi parasitic on scale insects. *Journal of the Department of Agriculture, Victoria* 2: 646–648.
- McNeill J, Barrie FR, Burdet HM, Demoulin V, Hawksworth DL, Marhold K, Nicolson DH, Prado J, Silva PC, Skog JE, Wiersma JH, Turland NJ (2006). International Code of Botanical Nomenclature (Vienna Code). *Regnum Vegetabile* 146. A.R.G. Gantner Verlag KG.
- Miyabe K, Sawada K (1913). On fungi parasitic on scale-insects found in Formosa. *Journal of the College of Agriculture, Tohoku Imperial University* 5: 73–90.
- Nees von Esenbeck, CDG (1817). System der Pilze und Schwämme. 1–334. Würzburg, Germany.
- Nelson PE, Toussoun TA, Marasas WFO (1983). *Fusarium* species: An illustrated manual for identification. 1–193. Pennsylvania State University Press, University Park, Pennsylvania.
- Nguyen HDT, Seifert KA (2008). Description and DNA barcoding of three new species of *Leohumicola* from South Africa and the United States. *Persoonia* 21: 57–69.
- Nirenberg HI (1976). Untersuchungen über die morphologische und biologische Differenzierung in der *Fusarium*-Sektion *Liseola*. *Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft* 169: 1–v + 1–117.
- Nirenberg HI, Samuels GJ (2000). *Nectria* and *Fusarium*. II. *Cosmospora zealandica* comb. nov. and its anamorph, *Fusarium zealandicum* sp. nov. *Canadian Journal of Botany* 78: 1482–1487.
- Nowrousian M, Kück U, Loser K, Weltling KM (2000). The fungal *acl1* and *acl2* genes encode two polypeptides with homology to the N- and C-terminal parts of the animal ATP citrate lyase polypeptide. *Current Genetics* 37: 189–193.
- O'Donnell K (1993). *Fusarium* and its near relatives. 224–233. In: *The fungal holomorph: mitotic, meiotic and pleomorphic speciation in fungal systematic* (Reynolds DR, Taylor JW, eds.). CAB International: Wallingford, UK.
- O'Donnell K, Sarver BA, Brandt M, Chang DC, Noble-Wang J, Park BJ, Sutton DA, Benjamin L, Lindsley M, Padye A, Geiser DM, Ward TJ (2007). Phylogenetic diversity and microsphere array-based genotyping of human pathogenic *Fusaria*, including isolates from the multistate contact lens-associated U.S. keratitis outbreaks of 2005 and 2006. *Journal of Clinical Microbiology* 45: 2235–2248.
- O'Donnell K, Sutton DA, Fothergill A, McCarthy D, Rinaldi MG, Brandt ME, Zhang N, Geiser DM (2008). Molecular phylogenetic diversity, multilocus haplotype nomenclature, and in vitro antifungal resistance within the *Fusarium solani* species complex. *Journal of Clinical Microbiology* 46: 2477–2490.
- O'Donnell K, Sutton DA, Rinaldi MG, Gueidan C, Crous PW, Geiser DM (2010). A novel multi-locus sequence typing scheme reveals high genetic diversity of human pathogenic members of the *Fusarium incarnatum*-*F. equisetii* and *F. chlamydosporum* species complexes within the U.S. *Journal of Clinical Microbiology* 47: 3851–3861.
- Palm ME, Gams W, Nirenberg HI (1995). *Plectosporium*, a new genus for *Fusarium tabacinum*, the anamorph of *Plectosphaerella cucumerina*. *Mycologia* 87: 397–406.
- Parkin J (1906). Fungi parasitic upon scale-insects (*Coccidae* and *Aleurodidae*): a general account with special reference to Ceylon forms. *Annals of the Royal Botanic Gardens, Peradeniya* 3: 11–82.
- Pascoe IG (1990). *Fusarium* morphology. I. Identification and characterisation of a third conidial type, the mesoconidium. *Mycotaxon* 37: 121–160.
- Petch T (1921). Studies in entomogenous fungi. *Transactions of the British Mycological Society* 7: 89–167.
- Posada D, Crandall KA (1998). Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.
- Radtkofer L (1863). Ueber die Verunreinigung eines der Münchener Trinkwasser. *Kunst- und Gewerbe-Blatt des polytechnischen Vereins für das Königreich Bayern* 49: 1–17.
- Ronquist F, Huelsenbeck JP (2003). MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
- Rossmann AY (1983). The phragmosporous species of *Nectria* and related genera. *Mycological Papers* 150: 1–164.
- Rossmann AY (1993). Holomorphic hypocrealean fungi: *Nectria sensu stricto* and teleomorphs of *Fusarium*. 149–160. In: *The fungal holomorph: mitotic, meiotic and pleomorphic speciation in fungal systematic* (Reynolds DR, Taylor JW, eds.). CAB International: Wallingford, UK.
- Rossmann AY, Samuels GJ (2005). Towards a single scientific name for species of fungi. *Inoculum* 56: 1–3.
- Rossmann AY, Samuels GJ, Lowen R (1993). *Leuconectria clusiae* gen. nov. and its anamorph *Gliocephalotrichium bulbilium* with notes on *Pseudonectria*. *Mycologia* 85: 685–704.
- Rossmann AY, Samuels GJ, Rogerson CT, Lowen R (1999). Genera of *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae* (*Hypocreales*, *Ascomycetes*). *Studies in Mycology* 42: 1–248.
- Saccardo PA (1883). *Sylloge fungorum omnium hucusque cognitorum* 2: 1–815 + i–lxix + 1–77.
- Samson RA (1974). *Paecilomyces* and some allied hyphomycetes. *Studies in Mycology* 6: 1–119.
- Samuels GJ (1976). A revision of the fungi formerly classified as *Nectria* subgenus *Hyphonectria*. *Memoirs of the New York Botanical Garden* 26(3): 1–126.
- Samuels GJ (1977). *Nectria consors* and its *Volutella* conidial state. *Mycologia* 69: 255–262.
- Samuels GJ, Doi Y, Rogerson CT (1990). *Hypocreales*. *Memoirs of the New York Botanical Garden* 59: 6–108.
- Samuels GJ, Hallett IC (1983). *Microdochium stoveri* and *Monographella stoveri*, new combinations for *Fusarium stoveri* and *Micronectriella stoveri*. *Transactions of the British Mycological Society* 81: 473–483.
- Samuels GJ, Lu B-S, Chaverri P, Candoussau F, Fournier J, Rossmann AY (2009). *Cyanonectria*, a new genus for *Nectria cyanostoma* and its *Fusarium* anamorph. *Mycological Progress* 8: 49–58.
- Samuels GJ, Rossmann AY, Lowen R, Rogerson CT (1991). A synopsis of *Nectria* subgen. *Dialonectria*. *Mycological Papers* 164: 1–48.
- Samuels GJ, Seifert KA (1987). Taxonomic implications of variation among hypocrealean anamorphs. 29–56. In: *Pleomorphic fungi: the diversity and its taxonomic implication* (Sugiyama J, ed.). Kodansha, Tokyo and Elsevier, Amsterdam.
- Samuels GJ, Seifert KA (1991). Two new species of *Nectria* with *Stilbella* and *Mariannaea* anamorphs. *Sydowia* 43: 249–263.
- Schoch C, Crous PW, Wingfield MJ, Wingfield BD (2000). Phylogeny of *Calonectria* and selected hypocrealean genera with cylindrical macroconidia. *Studies in Mycology* 45: 45–62.
- Schroers H-J, Gräfenhan T, Nirenberg HI, Seifert KA (2011). A revision of *Cyanonectria* and *Geejayessia* gen. nov. and related species with *Fusarium*-like anamorphs. *Studies in Mycology* 68: 115–138 (this issue).
- Schroers H-J, Geldenhuis MM, Wingfield MJ, Schoeman MH, Yen Y-F, Shen W-C, Wingfield BD (2005). Classification of the guava wilt fungus *Myxosporium psidii*, the palm pathogen *Gliocladium vermoeseni* and the persimmon wilt fungus *Acremonium diospyri* in *Nalanthamala*. *Mycologia* 97: 375–395.
- Schroers H-J, Lamprecht SC, O'Donnell K, Kammeyer PL, Johnson S, Sutton DA, Rinaldi MG, Summerbell RC (2009). Taxonomy and phylogeny of the *Fusarium dimerum* species group. *Mycologia* 101: 44–70.
- Schweinitz LD de (1822). *Synopsis fungorum Carolinae superioris*. Johann Ambrosius Barth, Leipzig (reprinted by J. Carner, Vaduz, 1976).
- Seifert KA (1985a). A monograph of *Stilbella* and allied hyphomycetes. *Studies in Mycology* 27: 1–235.
- Seifert KA (1985b). Notes on some apocryphal genera of synnematal Hyphomycetes. *Transactions of the British Mycological Society* 85: 123–133.
- Seifert KA (2001). *Fusarium* and anamorph generic concepts. 15–28. In: Summerell BA, Leslie JF, Backhouse D, Bryden WL, Burgess LW (eds): *Fusarium: Paul E. Nelson Memorial Symposium*. American Phytopathological Society, St. Paul, Minnesota.
- Seifert KA, Samuels GJ (2000). How should we look at anamorphs? *Studies in Mycology* 45: 5–18.
- Seifert KA, Stanley SJ, Hyde KD (1995). *Stilbella holubovae*, a new synnematal hyphomycete species on driftwood from the Philippines and South Africa. *Sydowia* 47: 258–262.
- Sivichai S, Jones EBG, Hywel-Jones N (2002). Fungal colonisation of wood in a freshwater stream at Tad Ta Phu, Khao Yai National Park, Thailand. *Fungal Diversity* 10: 113–129.
- Sukapure RS, Thirumalachar MJ (1966). Conspectus of species of *Cephalosporium* with particular reference to Indian species. *Mycologia* 58: 351–361.
- Sukumaran J, Holder MT (2010). DendroPy: a Python library for phylogenetic computing. *Bioinformatics* 26: 1569–1571.
- Summerbell RC, Gueidan C, Schroers H-J, Hoog GS de, Starink M, Iperen A van, Arocha Rosete Y, Guarro J, Scott JA (2011). *Acremonium* phylogenetic overview and revision of *Gliomastix*, *Sarocladium*, and *Trichothecium*. *Studies in Mycology* 68: 139–162 (this issue).
- Summerbell RC, Schroers H-J (2002). Analysis of phylogenetic relationship of *Cylindrocarpon lichenicola* and *Acremonium falciforme* to the *Fusarium solani* species complex and a review of similarities in the spectrum of opportunistic infections caused by these fungi. *Journal of Clinical Microbiology* 40: 2866–2875.
- Sutton BC (1977). Coelomycetes VI. Nomenclature of generic names proposed for coelomycetes. *Mycological Papers* 141: 1–253.
- Sutton BC (1986). Improvements on conidial themes. *Transactions of the British Mycological Society* 86: 1–38.
- Swofford DL (2003). PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Torzilli AP, Balakrishna S, O'Donnell K, Lawrey J (2002). The degradative activity of a lichenicolous *Fusarium* sp. compared to entomogenous species. *Mycological Research* 106: 1204–1210.

- Trabut L (1907). Un champignon parasite de la cochenille des orangers. *Bulletin agricole de l'Algérie et de la Tunisie* **13**: 32–108.
- Tubaki K, Booth C, Harada T (1976). A new variety of *Fusarium merismoides*. *Transactions of the British Mycological Society* **66**: 355–356.
- Tulasne ELR, Tulasne C (1861). *Selecta Fungorum Carpologia* **1**: 129–130.
- Tulasne ELR, Tulasne C (1865). *Selecta Fungorum Carpologia* **3**: 104–106.
- Weese J (1916). Beiträge zur Kenntnis der Hypocreaceen. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Klasse, Abt. 1*, **125**: 465–575.
- Wollenweber HW (1916/1924/1930). *Fusaria Autographice Delineata. Collectio Specierum ex Herbariis Variis Selectarum et ab Auctore Lectarum Cultarumque Synonymis et Excludendis Additis quas Determinavit, in Sectiones Digessit, Comparavit cum Hypocreaceis Analogis Praemissis ad Methodi Naturalis Normas et Culturae Purae Experientiam* H.W. Wollenweber **1**: i, 1–509; **2**: i, 510–659; **3**: i, 660–1100. Germany, Berlin.
- Wollenweber HW (1926). Pyrenomyceten-Studien. II. *Angewandte Botanik* **8**: 168–212.
- Wollenweber HW (1931). *Fusarium-Monographie. Fungi parasitici et saprophytici. Zeitschrift für Parasitenkunde* **3**: 269–516.
- Wollenweber HW, Reinking OA (1935). Die Fusarien: ihre Beschreibung, Schadwirkung und Bekämpfung. 1–355. Germany, Berlin.
- Yang ZH, Nielsen R, Goldman N, Pedersen A-MK (2000). Codon-substitution models for heterogeneous selection pressure at amino acid sites. *Genetics* **155**: 431–449.
- Zhang X-M, Zhuang W-Y (2006). Phylogeny of some genera in the *Nectriaceae* (*Hypocreales*, *Acomycetes*) inferred from 28S nrDNA partial sequences. *Mycosystema* **25**: 15–22.
- Zhdanova NN (1966). Rare and new species of *Dematiaceae* isolated from maize rhizosphere of various climatic belts of the Ukrainian SSR. *Mikrobiologicheskii Zhurnal, Kiev* **28**: 36–40. [in Russian]
- Zwickl DJ (2006). *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence data sets under the maximum likelihood criterion*. Ph.D. dissertation, The University of Texas at Austin.